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SOME NEW COLORADO DISCOMYCETES

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(WITH 6 FIGURES)

During the summers of 1929, 1930, 1933, and 1935, Mr. Ross W. Davidson made numerous collections of discomycetes in the Grand Mesa National Forest, Colorado. Two previous papers (**1**, **2**) have dealt with several species of *Sclerotinia* and a few of the Cenangiaceae from this locality: various other collections made by Mr. Davidson during these trips are discussed here. The specimens are deposited in the Mycological Collections of the Bureau of Plant Industry, and duplicates of those here listed as numbers 1, 2, 3, 4, and 6 are also in the Farlow Herbarium of Harvard University, the Herbarium of the New York Botanical Garden, and the Herbarium of the University of Michigan.

1. PROPOLIS FAGINEA (Schrad.) Karst. var. **atra**, var. nov.

Apothecia immersed in whitened areas of the wood, irregularly elliptical, occasionally circular, sometimes confluent, surrounded by the lacerated epidermis, brownish olive [1] to deep olive, greenish slate-black when dry, 1–3 × .7–1 mm.; asci cylindrical to cylindrical-clavate, 8-spored, 145–175 × 11–12 μ; spores uniseriate, rarely biseriate above, elongate-cylindrical, hyaline, straight or slightly curved, unicellular, biguttulate, thick-walled, granulose, 22–28 × 8–10 μ; paraphyses filiform, thickly branched and yel-

[1] Color terminology follows Ridgway, Color Standards and Color Nomenclature, Washington, D. C., 1912.

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lowish at the tips, forming a dense brownish or greenish mazaedium.

Ascomatibus immersis, ellipticalibus orbicularibusve, viridiatris, 1–3 × .7–1 mm.; ascis cylindricis vel cylindrico-clavatis, 145–175 × 11–12 μ; sporis plerumque uniseriatis, rare biseriatis, elongato-cylindricis, hyalinis, unicellularibus, granulosis, 22–28 × 8–10 μ; paraphysibus filiformibus, dense ramosis et luteis, mazaedium viridifuscum formantibus. Hymenio viridi-atro et ascis longioribus et angustioribus a speciei differt.

On old weathered wood of *Populus tremuloides,* Mesa Lakes, June 13, 1930, R. W. D. *222* (type), June 18, 1930, *324–a,* June 26, 1930, *455–a,* and July 18, 1930, *731.*

The color of the hymenium would not in itself constitute a character of sufficient importance for separating this as a variety of *Propolis faginea,* since although generally white or whitish, various other colors are noted by Rehm (**5**, p. 149–150): reddish, yellowish, brownish, etc. The much longer asci, however, are distinctive. *Propolis Betulae* Fuckel, which is included by Rehm as a variety of *P. faginea,* is described as having asci up to 162 μ in length, but in this species the spores are also much longer, 34–36 μ.

2. **Cenangella oricostata,** sp. nov. (FIG. 4).

Apothecia coriaceous, subglobose, sessile, depressed and radiately ridged at the apex, collapsing when old, emerging sometimes singly, more often in groups from cracks in the bark on a thin sclerotic layer, dark grayish olive, drying olivaceous black, 1–2 mm. diam., 1–1.5 mm. high, slightly furfuraceous; hymenium pallid neutral gray; asci cylindrical, short-pedicellate, 8-spored, 100–130 × 6–8 μ, wall 2.5 μ thick at the narrowed apex; spores fusoid-clavate, straight, 1–2-seriate, hyaline, uniseptate near the center, not constricted, upper cell broader and more rounded, lower narrower and acute, 12–15 × 3–4 μ; paraphyses hyaline, filamentous, not septate, longer than the asci, with two to three often recurved and slightly inflated branches at the tip; hypothecium prosenchymatous, pale brown; inner layer of the exciple thick, dark brown, of dense, thick-walled pseudoparenchyma; outer layer of olivaceous hyphae which break up in loose clumps scattered over the surface and become thickened into ridges radiating from the apex.

Apotheciis coriaceis, subglobosis, sessilibus, apice depressis et radiato-costatis, erumpentibus, griseo-olivaceis vel atro-olivaceis, 1–2 mm. diam., 1–1.5 mm. altis; hymenio pallide griseo; ascis cylindraceis, breve pedicel-

latis, 100–130 × 6–8 μ; sporis fusoideo-clavatis, 1–2-seriatis, hyalinis, 1-septatis, 12–15 × 3–4 μ; paraphysibus hyalinis, filamentosis, ramosis, apice leniter inflatis et recurvatis; excipulo atro-brunneo, crasso, filamentis olivaceis tecto.

On twigs of *Ribes Wolfii*, Mesa Lakes, June 16, 1935, R. W. D. *778*.

The fungus is apparently a member of the Cenangiaceae, superficially very similar to *Godronia*. Since the only genus in this family with two-celled spores is *Cenangella* Sacc., it is placed here, although *Cenangella* is not recognized by some recent authors. Von Höhnel (**3**, p. 369) considered *Cenangella*, as typified by *C. Fraxini*, synonymous with *Dermatella* Karst., while Nannfeldt (**4**, p. 82) includes both of these genera as synonyms of *Dermatea* Fries. It seems probable from the descriptions that various species of *Cenangella* should more properly be assigned to *Dermatea*, but the Colorado fungus differs widely from that genus in its unbranched, hyaline paraphyses and fusoid-clavate spores.

Although the asci and spores seem to be mature, no open apothecia were found in this collection. The fruiting-bodies may have a small round mouth like some species of *Godronia*, or more probably split into stellate lobes along the radiating ridges at the apex. These ridges suggest those in *Godroniopsis quernea* (Schw.) Diehl & Cash, but in *Cenangella oricostata* they are confined to the apical region and are much less pronounced.

Emerging from the cracks in the bark on the same basal stroma with the apothecia of the discomycete is a pycnidial fungus. The subglobose, non-ostiolate pustules, .7–1 mm. in diameter, and of the same color and texture as the apothecia, are completely filled with closely packed, bacillar, hyaline conidia, 2–4 × 1–1.5 μ. No conidiophores were observed.

Mr. Davidson has suggested that *C. oricostata* may be parasitic during early stages of development, since he found it fruiting either on dead areas of living stems or on dead twigs attached to living stems.

3. **Tapesia Lonicerae**, sp. nov. (FIG. 1).

Apothecia sessile, superficial, gregarious, soft-fleshy, 1–2.5 mm. diam., patelliform, irregularly contorted when dry, margin crenu-

late, inrolled, exterior black, raisin black or dark livid purple, densely setose at the margin, hairs bone brown or more rarely Diamine brown; hymenium pale neutral gray; asci cylindrical, narrowed at the apex, short-stipitate, 8-spored, 65–75 × 7–9 μ; spores obliquely uniseriate or biseriate, fusoid-clavate, uniseptate, not constricted, hyaline, 12–13.5 × 2–2.5 μ; paraphyses filiform, hyaline, non-septate, simple or branched near the base, the slightly inflated tips extending above the asci; hypothecium a loose prosenchymatic layer 50–100 μ; cortical layer pseudoparenchymatic, made up of dark, subglobose cells 5–8 μ in diameter; hairs brown, smooth, septate, 140–170 × 2.5–3 μ.

Apotheciis sessilibus, superficialibus, molle carneis, atris, patelliformibus, margine crenulato et setoso, 1–2.5 μ diam.; hymenio griseo; ascis cylindricis, apice attenuatis, octosporis, 65–75 × 7–9 μ; sporis oblique uniseriatis vel biseriatis, fusoideo-clavatis, uniseptatis, hyalinis, 12–13.5 × 2–2.5 μ; paraphysibus filiformibus, hyalinis, eseptatis, leniter inflatis; hypothecio prosenchymatico, 50–100 μ crasso; cortice pseudoparenchymatico; pilis brunneis, glabris, septatis, 140–170 × 2.5–3 μ.

On twigs of *Lonicera involucrata*, Mesa Lakes, June 16, 1935, R. W. D. *779*.

Both Rehm and Saccardo limit *Tapesia* to species of the Mollisiaceae having a subicle and 1-celled spores. Nannfeldt (**4**, p. 99), however, includes species with two-celled spores in the genus, so that according to his interpretation this fungus on *Lonicera* may be considered a *Tapesia*. Moreover, it does not readily fall in any of the genera of the family described with two-celled spores. *Niptera* has a smooth exciple, *Psorotheciopsis* biscuit-shaped spores, while the species of *Linhartia* are foliicolous, bright-colored fungi with paraphyses forming a mazaedium.

According to Mr. Davidson's records this species was abundant on *Lonicera involucrata* in the summer of 1935 soon after the melting of the snow. It appeared to be saprophytic on the outer bark at the base of living stems.

4. **Tapesia ribicola,** sp. nov. (FIG. 3).

Apothecia sessile, superficial, depressed-globose, then disc-shaped, irregularly contorted when dry, often hysteroid or triangular, gregarious, soft-fleshy, .6–1.5 mm. diam., exterior fuscous-black to black and smooth near the base, drab-gray to white and fimbriate at the margin; hymenium Court gray to Puritan gray; asci cylindrical-clavate, short stipitate, narrowed at the apex,

8-spored, 37.5–50 × 4.5–5 μ; spores biseriate, elongate-ellipsoid to clavate, hyaline, unicellular, straight or slightly curved, 7–11 × 1.5–2 μ; paraphyses filiform, hyaline, septate, unbranched, longer than the asci, not inflated; exciple pseudoparenchymatic, of small, dark, thick-walled, subglobose or hexagonal cells 5–7 μ in diam., densely covered toward the margin by brown, septate hyphae 2.5 μ diam., subhyaline at the tips.

Apotheciis gregariis, sessilibus, superficialibus, subglobosis demum patellatis, carneis-membranaceis, .6–1.5 mm. diam., base fusco-nigris, glabris, margine albo-griseis, fimbriatis; hymenio griseo; ascis cylindrico-clavatis, breviter pedicellatis, apice angustatis, octosporis, 37.5–50 × 4.5–5 μ; sporis biseriatis, clavatis, hyalinis, unicellularibus, 7–11 × 1.5–2 μ; paraphysibus filiformibus, hyalinis, septatis; textura excipuli pseudoparenchymatica, marginem versus hyphis pallide brunneis, 2.5 μ diam., obsitis.

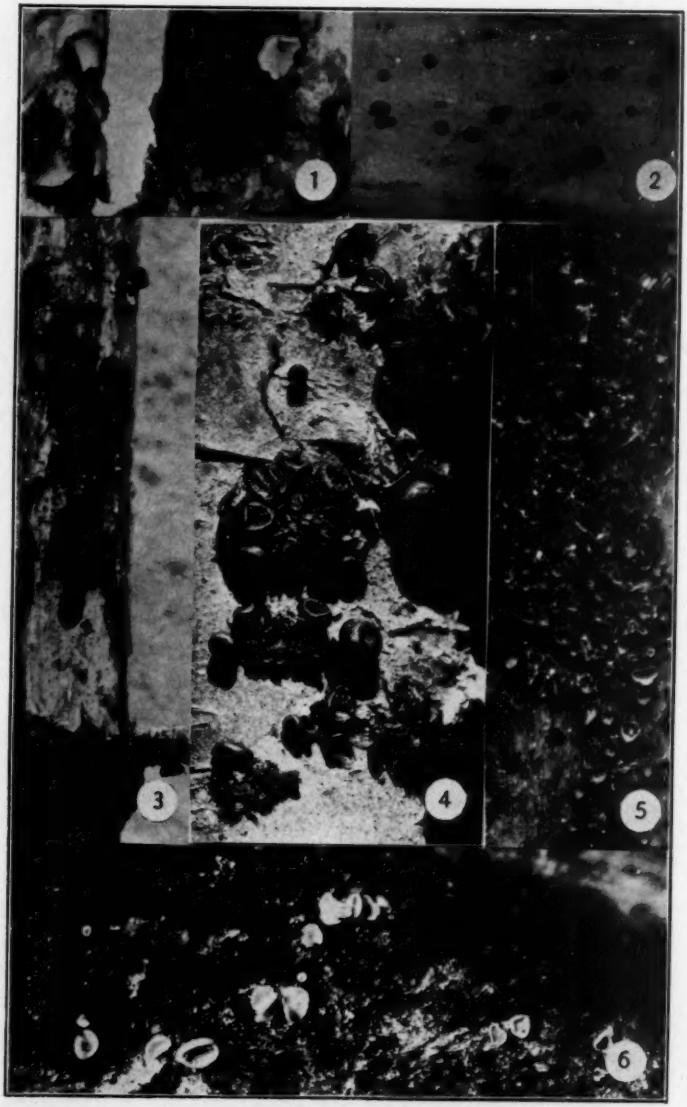
On twigs of *Ribes montigenum*, Mesa Lakes, June 15, 1935, R. W. D. *780* (type); on *Ribes* sp., Land's End, June 11, 1935, *775* and Buzzard Creek, June 17, 1935, *783*.

The spores of *Mollisia ribesia* Cooke & Peck and *Pyrenopeziza rimicola* (Karst.) Sacc., both of which occur on *Ribes*, are only 4–5 μ long. Among the species of *Tapesia* described, the most similar are *T. melaleucoides* Rehm and *T. coloradensis* Ellis & Ev., from which *T. ribicola* differs in the broader spores.

5. **Pezizella aurantiaca,** sp. nov. (FIG. 6).

Apothecia sessile, superficial, single or cespitose, at first subglobose, then cupulate to applanate, contorted by mutual pressure, waxy-fleshy, salmon-orange to orange-rufous, 1–2 mm. diam., pulverulent, hymenium concolorous; margin thin, delicately fimbriate, paler yellow, inrolled when dry; asci cylindrical-clavate, gradually narrowed at the base, wall thickened at the apex, 8-spored, 38–45 × 4–5 μ; spores cylindrical, straight or curved, 1–2-seriate, hyaline or pale greenish, unicellular with one oil drop in each end, 7–9 × 1.5–2 μ; paraphyses flexuous, septate, rarely branched near the base, gradually enlarged at the tip to 1.5 μ; exciple prosenchymatous, composed of pale reddish hyphae, the loose ends of which form the fimbriate margin.

Apotheciis sessilibus, singulis vel caespitosis, cupulatis applanatisve, ceraceis, aurantio-rubris, 1–2 mm. diam., minute luteo-pulverulentis, margine tenue, leniter fimbriato; ascis cylindraceo-clavatis, octosporis, 38–45 × 4–5 μ; ascosporis cylindricis, 1–2-seriatis, hyalinis vel subhyalinis, unicellularibus, biguttulatis, 7–9 × 1.5–2 μ; paraphysibus flexuosis, apice usque 1.5 μ latis.



FIGS. 1–6.

On bark of *Picea* sp., Grand Mesa, July 2, 1929, R. W. D. *132* (type), and July 21, 1929, *143*.

In general appearance this discomycete resembles *Pseudohelotium laricinum* Ellis & Ev., from which it differs microscopically. Kauffman's *Helotium sulphuratum* var. *Piceae*, which occurs on needles of *Picea Engelmanni* in Colorado, also has larger asci and spores.

6. **Belonium aggregatum,** sp. nov. (FIG. 5).

Apothecia sessile, urceolate to patellate, soft-fleshy, densely crowded on a more or less evident subiculum of pale olivaceous hyphae 3–4 μ diam., fuscous-black to olivaceous black, hymenium concolorous, margin paler and fimbriate, entire fungus black when dry; asci cylindrical-clavate, slightly narrowed at the apex, pore blue with iodine, 8-spored, 50–65 $\times$ 6–7 μ; spores 1–2-seriate, clavate to cylindrical, 1–3-septate, not constricted, 13–15 $\times$ 2.5–3 μ; paraphyses filiform, unbranched, septate, hyaline, slightly enlarged at the apex to 2 μ; exciple prosenchymatic, of thick-walled, olivaceous hyphae which become subhyaline and fasciculate at the margin.

Apotheciis sessilibus, urceolatis dein patellaribus, carnosulis, in subiculo hypharum olivacearum, 3–4 μ diam. dense aggregatis, fuscis vel olivaceo-atris, hymenio concolore, margine pallidiore fimbriato; ascis cylindrico-clavatis, apice attenuatis, 50–65 $\times$ 6–7 μ; sporis hyalinis, 1–2-seriatis, clavatis vel cylindricis, 1–3-septatis, 13–15 $\times$ 2.5–3 μ; paraphysibus filiformibus, simplicibus, septatis, hyalinis, apice 2 μ diam.; textura excipuli prosenchymatica, olivacea.

On decorticated wood of *Populus tremuloides,* Mesa Lakes, July 18, 1930, R. W. D. *734–a* (type), and June 18, 1930, *341*; on weathered wood of *Salix*, June 14, 1930, *240–a*.

The dark subicle is sometimes nearly absent; when present it gives the fungus the appearance of a *Trichobelonium*, from which it differs in the shorter spores and prosenchymatous texture of the exciple.

FIGS. 1–6. 1, *Tapesia Lonicerae* on *Lonicera involucrata*, R. W. D. *779*, $\times$ 5; 2, *Belonium inconspicuum* on *Abies* sp., R. W. D. *500–a*, $\times$ 5; 3, *Tapesia ribicola* on *Ribes montigenum*, R. W. D. *780*, $\times$ 5; 4, *Cenangella oricostata* on *Ribes Wolfii*, R. W. D. *778*, $\times$ 5; 5, *Belonium aggregatum* on *Populus tremuloides*, R. W. D. *734–a*, $\times$ 10; 6, *Pezizella aurantiaca* on *Picea* sp., R. W. D. *132*, $\times$ 5. Photographic negatives by M. L. F. Foubert.

7. **Belonium inconspicuum,** sp. nov. (FIG. 2).

Apothecia sessile, superficial, single, smooth, patellate, thin-membranous, .2–.5 mm., fuscous-black, hymenium drab; asci clavate, short-pedicellate, wall thickened at the apex, pore blue with iodine, 50–65 × 8–10 μ, averaging 50 × 7 μ, 8-spored; spores ellipsoid to broad-clavate, obliquely 1-seriate to irregularly biseriate, hyaline, 3-septate, not constricted, 12–15 × 4–5 μ; paraphyses septate, branched, with globular, olive-brown, glutinous tips 5 μ diam., forming a greenish-brown mazaedium; exciple prosenchymatous, hyaline at the base, gradually elongated and brown toward the margin.

Apotheciis sessilibus, superficialibus, singulis, patelliformibus, tenuiter membranaceis, .2–.5 mm. diam., brunneis; hymenio pallide alutaceo; ascis clavatis, breve pedicellatis, octosporis, 50–65 × 8–10 μ; sporis ellipsoideo-clavatis, 1–2-seriatis, 12–15 × 4–5 μ; paraphysibus septatis, ramosis, apice brunneis, mucosis, usque 5 μ latis, mazaedium olivaceum formantibus.

On decorticated twigs of *Abies*, Grand Mesa, July 2, 1930, R. W. D. *500–a*.

On account of its prosenchymatous exciple, this fungus belongs in the Helotiaceae where the 3-celled spores place it in *Belonium*. According to Rehm, species of this genus have hyaline paraphyses, varying widely in form: lanceolate, filiform, swollen at the tip, simple or branched. In this material the paraphyses resemble those of *Dermatea*, but the thin membranous texture distinguishes it from members of that and related genera.

Several species of *Belonium* are described by Velenovsky (**6**, p. 176–177) on conifers, but all differ in size, color, dimensions of spores and character of the paraphyses.

8. LACHNUM CALYCULAEFORME (Pers.) Karst.

Apothecia short-stipitate to sessile, scattered or gregarious, fleshy-waxy, densely tomentose, subglobose, Verona brown to snuff brown, 1 mm. diam., .7–1 mm. in height, opening small, circular, margin fimbriate, hymenium pale vinaceous-fawn to pinkish buff, stipe short, often lacking; asci cylindrical, apex obtuse, 8-spored, 55–60 × 5–7 μ; spores biseriate above, uniseriate below, elliptical-clavate, hyaline, unicellular, 8–10 × 1.5–2 μ; paraphyses hyaline, stiff, rather stout, longer than the asci, septate, unbranched, swollen to 3 μ near the narrowed tips; exciple pale, prosenchymatous, densely covered by bright yellow-brown,

tangled, verrucose, septate, flexuous hairs, 200 × 3–5 μ, frequently bearing crystals on the pale tips.

On decorticated wood of *Salix*, Mesa Lakes, June 14, 1930, R. W. D. *240*, June 18, 1930, *314*; on *Populus tremuloides*, Mesa Lakes, June 18, 1930, *340–a*, July 14, 1930, *652*, July 18, 1930, *734–b*.

This material was at first tentatively determined as *Dasyscypha albolutea* (Pers.) Rehm, but study of a specimen of the latter (Rehm Ascomyceten *1720*, on *Ulmus*, leg. Vogel, Germany) demonstrates that in the Colorado fungus the hairs are darker and rougher and the asci and spores larger. The apothecia are also more frequently stipitate and globose than in *D. albolutea*. *Dasyscypha Fairmani* Rehm has still larger spores and smooth hairs.

Dasyscypha albolutea (Pers.) Rehm, *Lachnum calyculaeforme* (Pers.) Karst. and *L. fuscofloccosum* Rehm are very similar in general appearance, size of spores and in the slender paraphyses which appear to be intermediate between the lanceolate form characteristic of *Lachnum* and the filiform type of *Dasyscypha*. In this regard, Rehm (**5**, p. 898) describes *L. calyculaeforme* var. *latebricola* as follows: "Paraphysen theils fädig, theils lanzettförmig spitz, die Schläuche überragend." The Colorado specimens examined agree with European material of *L. calyculaeforme* (Krypt. Exs. Vind. *1617*, on *Betula alba*, coll. Keissler, Carniola). The hairs in *Dasyscypha albolutea* are nearly hyaline and echinulate, while those of *Lachnum fuscofloccosum* Rehm are smooth and brown. The three species are difficult to distinguish and it is possible that examination of more abundant material may prove them to be identical.

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A NEW PREDACIOUS FUNGUS

J. S. KARLING

(WITH 5 FIGURES)

In the fall of 1935 while collecting species of Characeae for inoculation with *Diplophlyctis intestina* numerous thalli of *Sommerstorffia spinosa* Arnaud. and *Zoophagus insidians* Sommer. were found on filaments of *Nitella flexilis*. These aquatic fungi are to some degree epiphytic on a wide variety of algal filaments, and derive their nourishment from species of rotifers which they capture and devour. The latter fungus seems to be fairly abundant and has been found several times in Europe and thrice in America (**7**, **8**, **9**), while *Sommerstorffia spinosa*, according to the literature, appears to be more limited and has apparently been reported only twice each in Bulgaria (**2**, **10**) and the United States.

The *Nitella flexilis* filaments on which our material occurred were collected in a small brook at Arcola, New Jersey, in early October and grown in battery jars in the laboratory throughout the fall and winter. In the course of time, however, *S. spinosa* and *Z. insidians* gradually disappeared as the supply of rotifers was exhausted, and it was not until approximately a month later that an effective method of growing *Monostyla* was developed which insured a constant supply of food. Accordingly, vials containing rotifers were added from time to time to the jars of *Nitella* in hopes of reviving the fungi. *Sommerstorffia spinosa* failed to reappear, and only a few mycelial fragments of *Z. insidians* were found. In the course of this search, however, another rotifer-capturing species was discovered which proved to be strikingly different from *Z. insidians* in two respects. Whereas the latter possesses only short peg-like branches for the capture of its prey this new species develops in addition elongated, tenuous predacious tentacles at the tips of the pegs. Furthermore, its mycelium, in the early and preabsorptive condition, is somewhat smaller in diameter than that of *Z. insidians*. These differences

have been so constant and marked in all filaments so far observed that there can be no doubt but what we are dealing with a new species. However, with the exception of these two chief characteristics the fungus is essentially similar to *Z. insidians* and undoubtedly belongs in the same genus. Accordingly, I am proposing the specific name *tentaclum* for this new member, with the view of emphasizing its outstanding structural character.

Zoophagus tentaclum sp. nov.

Mycelium filamentous, greatly extended, 3–6 μ in diameter, hyaline, branched and continuous; possessing numerous relatively short specialized lateral branches, 15–35 μ in length and 3–5 μ in

FIG. 1. Thallus of *Z. tentaclum* before and after capturing its prey.

diameter, which bear one to five tenuous, predacious tentacles at the apex. Cytoplasm in the tips of the short lateral hyphae highly refractive; tentacles, 10–17 μ in length and 1.5 to 2 μ in diameter, and terminated by a small knob. Conidia or gemmae produced at the end of the long hyphae in acropetal succession, 40–80 μ in

length and 3–6.5 μ in diameter. Growing loosely epiphytic on *Nitella flexilis;* predacious and parasitic on species of *Monostyla, Diostyla,* etc.

STRUCTURE OF THE MYCELIUM

The thallus of *Z. tentaclum* is definitely filamentous and greatly extended as is shown in figure 1*A*. It appears to be strictly external and in no cases so far observed has it been found to penetrate and ramify the *Nitella* cells as Sparrow has described for *Z. insidians.* Most of my material has been found on *Nitella internodes* which had previously been killed by cooking in water and thus were in a state of disintegration. Even under such conditions the fungus mycelium remained entirely external. It appears thus to have merely a loose epiphytic relationship with the alga, and no differentiated anchoring organs such as are often seen in *Sommerstorffia* have been observed. In its early stages and particularly when the food supply is scant it may often consist of only a single isodiametric elongated filament with numerous short side branches which bear the predacious tentacles, figure 1*A*, but as it matures and captures a large number of rotifers it begins to grow very rapidly and branch freely so as to form often a conspicuous weft around the *Nitella* cells. In figure 1*A* is shown a filamentous thallus with eight short branches which was found growing rather closely applied to a *Nitella* internode. After this drawing had been made the specimen was removed from the slide and placed in a vial full of *Monostyla* and other rotifer species. When examined again under the microscope two hours later, it had captured four rotifers, three of which were still actively kicking and jerking to escape. Its appearance and structure seventy-two hours later is shown in figure 1*B*. It has elongated considerably, developed five long lateral branches, numerous additional organs of prey, and captured eighteen rotifers. Under such conditions of food supply, the mycelium increases markedly in diameter towards the growing end and may become quite irregular in outline. Figure 2 shows the terminal portion of a richly branched thallus with ten captive rotifers in various stages of consumption. The irregular outline and increased diameter of the mycelium is particularly evident in this figure.

As to structure, the mycelium is non-septate and continuous, branched, hyaline and varies from 3 to 6 μ in diameter. Its content is finely granular with numerous suspended round, irregular, rod-shaped and elongated bodies, granules and globules. These are essentially similar to those described by Sommerstoff in the cytoplasm of *Z. insidians,* but apparently not as large and obvious. Whether or not they are chondriosomes remains to be determined

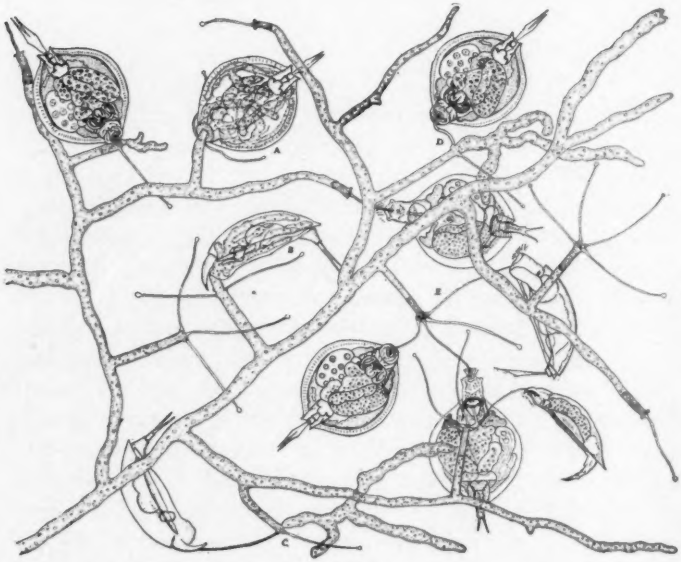

FIG. 2. An enlarged terminal portion of the mycelium with ten captive rotifers.

from study of fixed and stained material. Streaming and circulation of the cytoplasm is usually quite marked but not as conspicuous as in *Z. insidians.* In this process the suspended bodies are passively carried along, although in many instances it may appear as if they possess independent motion. This, it seems to me, is an optical illusion, because the medium in which they are suspended is often so homogeneous optically that its movement may be readily overlooked. As a consequence the various bodies frequently seem

to be moving of their own accord. So far no nuclei have been recognized in living material.

The lateral branches which bear the tentacle vary from 15 to 36 μ in length, depending to some degree on the supply of food; and with the exception of the apex, have the same appearance as the remainder of the mycelium. Before extensive feeding begins they are usually slightly smaller in diameter than in the main filament. When the mycelium lies closely applied to a *Nitella* internode they are formed on only one side and at right angles to the main axis, so that they stand out and away in an erect position. On the other hand, when the thallus becomes detached they develop on all sides, particularly if the supply of food is abundant. The cytoplasm in the upper end and apex of these short branches is quite different optically from that in the remainder of the thallus. It appears more dense and sharply refractive, and in this respect it is similar to that in the predacious branches of *Z. insidians* and *S. spinosa*. The tentacles vary from one to five, but four is the predominating number, according to my observations. They may be borne terminally on the main axis of the mycelium, figures 1 and 2, as well as on the short lateral branches, and branch occasionally, figure 3*J*. They vary from 10 to 17 μ in length and 1.5 to 2 μ in diameter, and are usually terminated by a small knob, which apparently plays an important rôle in the capture of rotifers. As a general rule they are slightly swollen at the base. The tentacles are filled with a homogeneous hyaline cytoplasm, which usually does not appear as refractive as that in the tip of the branch on which they are borne; it is thus still uncertain whether or not this modified cytoplasm always extends into the tentacles themselves. At least they are generally free of suspended bodies and granules.

Successive developmental stages of the side branches and tentacles are shown in figure 3*A* to 3*F*. The former begin as lateral buds on the mycelium, figure 3*a*, which rather rapidly attain a length varying from 15 to 36 μ if the thallus is well nourished. Subsequently the apex becomes somewhat blunt, figure 3*D*, and the initials of the tentacles begin to appear as small papillae. In the meantime, the cytoplasm in the apex begins to show its refractive character and density. The incipient tentacles are at first slightly pointed at the apex, figure 3*E*, but as they attain their mature

length the tips enlarge to form the characteristic knobs, figure 3*F*. These rarely become more than one and a half times the diameter of the filaments which bear them. Figure 3*G* shows a portion of a terminal branch with a single tentacle and the rudiments of three others, while figure 3*H* illustrates a lateral branch with only two tentacles. The appearance of tentacles when viewed from above is shown in figure 3*I*. This latter figure shows clearly the manner in which the tentacles stand out from the short hyphae. At maturity they appear to be quite resilient and flexible in texture. They may readily be bent by a micro-dissection needle, and when

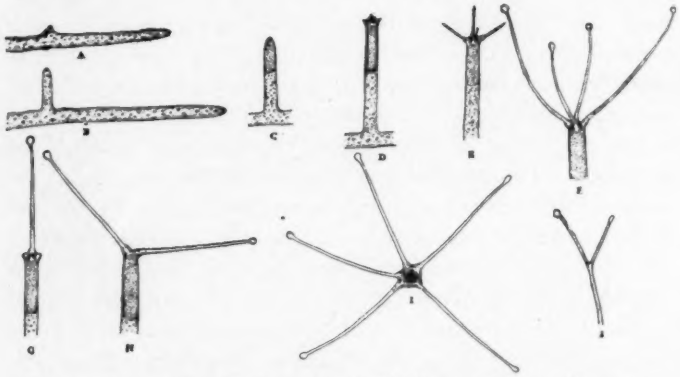

FIG. 3. Stages in the development and variations of the lateral branches and tentacles.

the pressure is released, they spring back into their original positions. In no cases so far observed have they been found to be elastic or contractive. That they are extremely tough and resistant is attested by their durability after capturing a rotifer. For more than an hour the captive animal makes every effort to free itself by jerking, turning over, and clamping down repeatedly on the tentacle, and although the latter may thus become twisted and bent back and forth an indefinite number of times it seldom breaks.

FEEDING HABITS OF ZOOPHAGUS TENTACULUM

Each of the tentacles described above is capable of capturing a rotifer, and it is at once obvious that the effectiveness of *Z. ten-*

taclum is thereby increased many times beyond that of *Z. insidians* and *Sommerstorffia spinosa.* In two instances I have observed as many as three rotifers attached to a single branch bearing four tentacles, figure 2*E*, but such cases are quite rare. As is shown in figures 3*F* and 3*I* the tentacles usually stand out somewhat like fingers on the palm, and are thus enticing bait for any foraging species of *Monostyla.* As the feeding rotifer comes in contact with a tentacle the latter is drawn into the mouth by the beating cilia, and the animal thus finds itself caught as it tries to move away. According to my observations, the tentacle does not appear to be distasteful or immediately poisonous to the rotifer, for the latter does not become aware of its presence until it begins to swim away. In many instances the rotifers may continue feeding in the immediate vicinity for some time after being caught. Quite frequently one or all of the tentacles down to the apex of the lateral branch may be engulfed, figures 2*A* and 2*B*. As to the actual process by which the capture is effected we have very little concrete knowledge. In *Z. insidians* and *S. spinosa* the capturing organs are reported by Sommerstorff (**6**), Arnaudow (**1**, **2**), Mirande (**5**), and Sparrow (**7**) to exude a drop of sticky fluid which adheres to the tip, and as the rotifer engulfs the apex it thereby becomes caught. Although the actual capture of more than a hundred rotifers have so far been observed, I have yet failed to find any exuded drops in connection with the tentacles of *Z. tentaclum.* I have also failed to observe them in *Z. insidians.* It is not inconceivable, however, that the knobs in the former species may be punctured when eaten, and thereby release an adhesive fluid. If such is the case it is obvious that this fluid must be extremely tenacious in order to hold the rotifers until they die. So far no contraction of the tentacles has been observed to occur before or after the capture.

Death of the prey usually ensues in less than two hours. To date one hundred and twenty-six captures have been seen, and careful records have been kept of the length of time the captives remained alive. The shortest execution observed required seventy, and the longest one hundred and eighteen minutes. Death is thus a comparatively slow process. As has been described above, the rotifer is quite active and vigorous when first caught, but after

approximately three-quarters of an hour has elapsed it becomes more quiescent with only occasional flips of the tail. Continual efforts, however, are made to regurgitate the engulfed tentacle, which are frequently accompanied by spasmodic contraction of the viscera. Finally, as the rotifer dies the muscles relax and the mouth usually opens wide. As to the successive internal cytological changes which occur in the rotifer as it is being consumed, very little is known at the present time. They doubtless vary

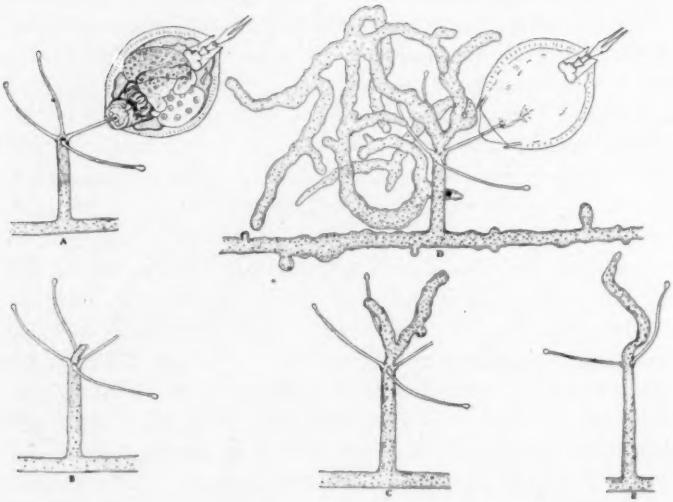

FIG. 4. Successive stages in the development of "external" hyphae in the vicinity of a captured rotifer.

somewhat with the type and degree of invasion. Abundant material in all stages of infection and consumption has been fixed, and a report of the changes together with cytological study of the parasite itself will be made later.

If the rotifer has engulfed a tentacle down to the branch, the latter generally grows into the mouth, figure *2A* and *2B*, and forms a tangled and coiled mass of tubular hyphae which consume the body contents. These hyphae are usually somewhat smaller in diameter than the main axis of the mycelium and are to be regarded in most cases as haustoria. On the other hand, when only

the tip and knob of a tentacle is engulfed the branch may not enter the rotifer at all but elongate and branch on the outside. In such cases it is obvious that the tentacles act not only as organs of prey but haustoria or absorbing organs as well. Figure 4*A* shows a rotifer which has recently been captured at the end of a tentacle. Within an hour and a half, even before the animal was completely dead, a noticeable change appeared in the tip of the branch, as is shown in figure 4*B*. It is slightly elongated and has put forth a small bud beyond the base of tentacles. The same branch three hours later is shown in figure 3*c*. Its appearance six days later is shown in figure 4*D*. The entire rotifer with the exception of the outer chitinous shell has been consumed, and the tip of the branch has been transformed into a snarl of elongated, branched, irregular and gnarled hyphae. Likewise, the main axis of the mycelium has increased in diameter and become uneven and bumpy in contour quite similar to that of *Z. insidians* as described by Gickehorn. Furthermore, an adjacent short hypha, figure 4*E*, bearing two tentacles has also begun to elongate at the apex. The cytoplasm in the hyphae and main mycelium under such conditions usually appears denser and more homogeneous, while the streaming becomes sluggish and almost imperceptible. The preying tentacle in figure 4*D* has undergone but little change; it is frayed at the end, and somewhat extended. The development of external hyphae such as is shown in figure 4 is the most extended of any so far observed and is thus exceptional in many respects. In the majority of cases the development has not proceeded much beyond the stages shown in figures 2*C* and 2*D*.

In a few thalli the tentacle bearing branches may fail to develop either intra- or extramatrical hyphae, and the absorbed food is used for the growth and development of the thallus as a whole. In such cases a marked change is soon visible. The mycelium begins to elongate, increase in diameter and branch, as is shown in figure 2. Sometimes the other branches which bear the tentacles may be stimulated to intercalary growth, and may occasionally elongate at the apex as in figure 4*E*.

As to its hosts, *Z. tentaclum* has been found chiefly on species of *Monostyla,* particularly *M. solidus,* although members of *Distyla* have twice been found captives. From the data at hand,

it thus appears to be somewhat more limited in host range than *Z. insidians,* which according to Sommerstorff, Arnaudow, and Mirande is capable of capturing and devouring species of four rotifer genera and one infusorian. I have frequently found species of *Amoeba, Actinophrys, Actinosphaerium, Paramoecium,* etc., engulfing the tentacles without being caught or suffering any serious consequences. *Amoeba proteus* has once been observed to engulf and absorb the elongated gemmae or conidia. The unusual method which these predacious fungi employ in capturing their hosts suggests that the structural relationships between the two may be rather specific, and particularly adaptive on the part of the parasites. In some of the more highly specialized flowering plants, according to current conceptions, the floral parts are adapted to insect pollination, and it is not at all inconceivable that the spines, tentacles and adhesive fluid, if the latter proves to be such, in these fungi have also gradually evolved and adapted themselves specifically to the mouth parts of rotifers.

CONIDIA

Numerous elongated and somewhat spindle-shaped gemmae or conidia have frequently been found in my cultures of *Z. tentaclum.* Their formation and development is fundamentally similar to the same process described by Arnaudow for *Z. insidians,* with but minor variations. According to my observations, conidial production occurs only after a prolonged feeding period in which the mycelium appears to become unusually well nourished. This is evidenced by its somewhat irregular contour, larger diameter, and the marked density and sluggishness of the cytoplasm. Gemmae are formed only at the terminus of the main mycelium or the lateral branches, other than those which bear the tentacles. In figures 5*A* to 5*I* I have illustrated the progressive developmental stages at the end of a lateral branch. Conidial bearing branches may often be recognized in their early stages by the presence of a constriction near the apex. This results in the development of a bud-like growth at the tip, which becomes the rudiment of a conidium. As it elongates it usually increases markedly in diameter at the equator, and the constriction or isthmus of the branch

becomes more pronounced and conspicuous. A later stage is shown in figure 5*C*. The conidium is considerably longer and thicker with the apical end distinctly rounded, while the isthmus has become narrower and longer. The final separation of the conidia from the branch or conidiophore is quite unusual and characteristic, figures 5*D* to 5*F*. The isthmus constricts more and more until practically no cytoplasm is to be seen in it, and finally

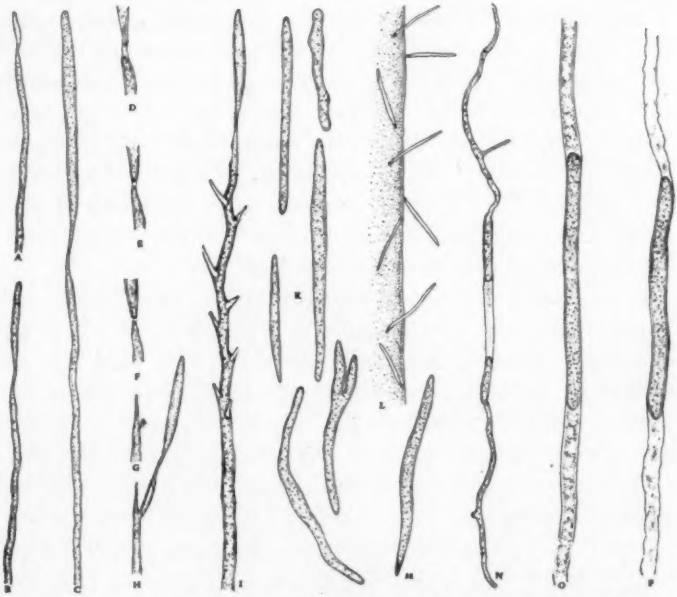

FIG. 5. Stages in the formation, structure, habitat and germination of gemmae or conidia.

the walls seem almost to merge. The cytoplasm in the basal end of the conidium and the apex of the conidiophore then retract slightly, figure 5*E*, forms a definite membrane which becomes modified and eventually seals up the ends of the two. The walls of the isthmus then break at a point midway between, and the conidium is thereby abstricted, as is shown in figure 5*F*. It is to be noted that no cross walls are formed in the process. Additional conidia may be formed on the same branch. These begin similarly

as small buds shortly behind the pointed apex of the conidiophore, figure 5*G*, and mature in the same fashion as the primary conidium. As a result of the acropetal succession of conidia an old conidiophore may have a number of sharp peg-like branches along its apical end, which freuently gives it a somewhat zigzag appearance, as is shown in figure 5*I*.

As the conidia separate from the conidiophores they may be carried away in the water. With further development the basal end increases in diameter and loses its sharply pointed appearance, so that it is now and then difficult to differentiate between the two ends, figure 5*K*. At maturity the gemmae are usually elongated and spindle-shaped, as is shown in figure 5*K*. Occasional branched ones still attached to the conidiophore have also been observed. They may vary from 40 to 80 μ in length and 3 to 6.5 μ in diameter. Their cytoplasm appears quite dense without any conspicuous vacuoles and imbedded refractive bodies. No streaming of the cytoplasm has so far been seen.

In a number of microscopic mounts numerous conidia have been found standing out at right angles to the internode of *Nitella* as if definitely attached, as is illustrated in 5*L*. The basal ends of these were distinctly wedge-shaped, and filled with a sharply refractive substance, figure 5*M*, and frequently had the appearance of rudimentary anchoring organs. It is thus not inconceivable that in the early stages of development species of *Zoophagus* may be more epiphytic in their habitat than is generally believed.

Numerous germination stages of the conidia have been found, figure 5*N*. The germ tubes may arise at both ends, and occasionally in the middle. They grow out into elongated filaments, and soon develop short lateral branches which bear the tentacles. Extensive branching of the main axis, however, does not generally occur until the food supply is augmented from captive rotifers.

Another method of reproduction or perpetuation of the thallus frequently occurs as it gets older. Quite often portions of the mycelium may die or get killed, which leaves regions in between alive, figure 5*O*. The protoplast immediately develops membranes at the ends of the living sections, which shortly take on the character of convex walls, as Sommerstorff has described in *Z. in-*

sidians. The living portions of the mycelium are thus shut off, and as the remainder of the thallus disintegrates they lie free in the water or on the *Nitella* cells and look strikingly similar to blunt conidia, figure 5*P*.

So far neither zoösporangia, zoöspores, oögonia nor antheridia have been found. However, the general structural characteristic and method of feeding are so similar to those of *Z. insidians* that the same type of asexual and sexual reproduction will doubtless be found to prevail in this species as well.

SUMMARY

1. *Zoophagus tentaclum* has been found growing loosely epiphytic on filaments of *Nitella flexilis* from Arcola, New Jersey, as a predacious parasite of species of *Monostyla* and *Distyla*.

2. The thallus consists of an extended, hyaline, continuous, branched, and filamentous mycelium with relatively short, specialized lateral branches which bear from one to five elongated tenuous predacious tentacles at their apices.

3. The tentacles are terminated by a small knob, and are thus the specialized organs for capturing rotifers. As they are drawn into the mouth of the feeding animal, the latter becomes caught in some manner and is unable to break away, and death ensues in less than two hours. The tentacles may also serve as haustoria or organs of absorption when no hyphal haustoria are developed in the captured rotifer.

4. When the tentacles are engulfed down to the apex of the short specialized branches, the latter grow into the mouth of the rotifer and develop highly coiled and richly branched tubular haustoria, which absorb the contents of the host in a few days.

5. Cylindrical and spindle-shaped gemmae or conidia are produced in acropetal succession at the ends of elongated lateral and terminal branches.

6. Neither zoösporangia, antheridia, nor oögonia have so far been observed.

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EVIDENCES FOR THE POSSIBLE OCCURRENCE OF SEXUALITY IN DIPLOPHLYCTIS

F. K. Sparrow, Jr.

(with 2 text figures)

The purpose of this note is to record the fact that there are evidences which seem to point to the existence of sexuality in the chytridiacean genus *Diplophlyctis*.

The morphology and development of this striking inhabitant of dead cells of the Characeae have been the object of study by several investigators, notably Zopf [1] and more recently Karling.[2] The latter's series of observations on the sequence of events in the establishment of the thallus (which the writer can confirm) are particularly noteworthy. However, neither of these investigators presented any material which might help us answer the most pertinent question in the life-history of this fungus, namely: Is formation of the resting spore preceded by any type of sexual process?

In material of *Nitella*, obtained in October 1934 by the writer from Ithaca, N. Y., through the kindness of Prof. W. K. Stone, there occurred an abundance of resting spores in all stages of development. In examining this material it was found that, under particularly good optical conditions and a favorable disposition of the opaque host contents, in addition to the typical large, apophysate, spiny resting structures, there could also be detected minute, scarcely visible thalli. These were found in almost constant association with *maturing* resting spores (not old ones with a disintegrating rhizoidal system). They were about 10 μ high by 5 μ in diameter, possessed a rhizoidal system of limited extent, with or

[1] Zopf, W. 1884. Zur Kenntniss den Phycomyceten I. Zur Morphologie und Biologie der Ancylisteen und Chytridiaceen, zugleich ein Beitrag zur Phytopathologie. Nova Acta Leop. Deutsch. Akad. Nat. **47**: 141.

[2] Karling, J. S. 1928. Studies in the Chytridiales II. Contribution to the life history and occurrence of *Diplophlyctis intestina* (Schenk) Schröt. in cells of American Characeae. Am. Jour. Bot. **25**: 204.

without an apophysis, and in every way resembled the very immature thalli. When associated with fully mature resting spores they were empty, adding further to their invisibility.

In particularly favorable specimens it could be seen that there is a definite connection between the rhizoidal systems of these two types of structures (FIG. 1). This anastomosis is usually achieved

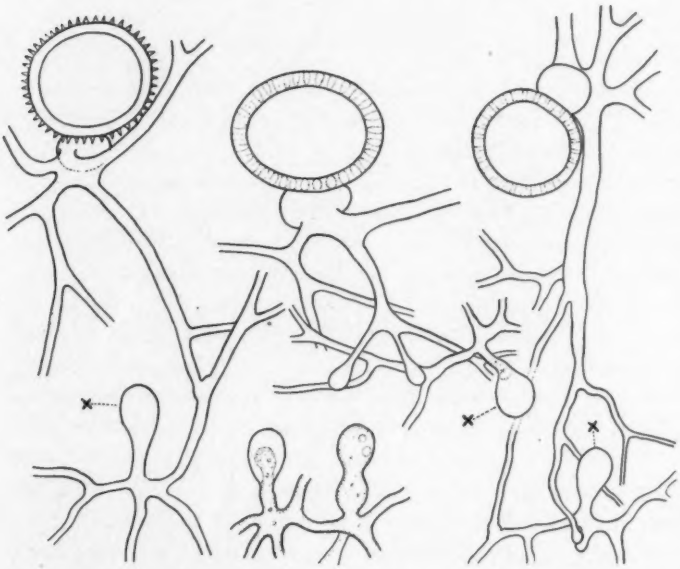

FIG. 1. Four typical instances of association and anastosmoses of thalli in *Diplophlyctis intestina*. The smaller thalli which have apparently contributed their content to the formation of the resting spore are marked "x." × 1200.

by the rhizoid of the larger body which may fuse laterally with one or two rhizoids of the other; less often the reverse situation is observed. Sometimes the rhizoid of the receptive thallus connects directly with the apophysis or point of origin of the rhizoids of the smaller plant (FIG. 2). At the point of contact, the rhizoid is frequently slightly distended as if a minute appressorium had been formed. Observations would also seem to indicate that connection of the two thalli and transference of material may take place at a

very early stage in thallus development. In many cases the contributing thallus has apparently been emptied just after the formation of the rhizoids and prior to the formation of the apophysis. Such empty thalli often possess a foamy content or a minute, refractive globule.

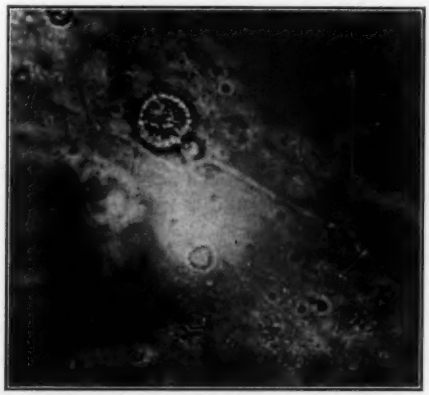

FIG. 2. Photomicrograph of association of a resting spore of *Diplophlyctis* and a smaller thallus. One of the rhizoids of the resting spore has made contact with the rhizoidal system of the smaller thallus, indicated by an arrow. × 357.

The actual transference of materials into the receptive thallus could not be detected. For this reason, but more especially because of the fact that the structures involved are so minute, the writer feels that further observations are needed by other investigators before it can be said definitely that this association and union of thalli is, as he strongly suspects, the result of a *Siphonaria*-like type of sexuality.

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THE USE OF ULTRA-VIOLET IRRADIATED CULTURE MEDIA FOR SECURING BACTERIA-FREE CULTURES OF SAPROLEGNIA [1]

IRVIN H. BLANK AND WESLEY N. TIFFNEY

(WITH 1 FIGURE)

In almost all mycological work it is essential to secure and to maintain pure cultures of the fungi being investigated. Yet in many cases, cultures of the fungi, free from bacteria, are extremely difficult to obtain. This preliminary step in an investigation is often tedious and disproportionately time-consuming and hence the major objective of one's research is often long delayed.

The Saprolegniaceae, as a group, are especially troublesome to isolate. This difficulty arises because of the following conditions: these fungi occur in nature accompanied by large numbers of bacteria; usually the fungi themselves are slower in growing than the bacteria; the fungi, when grown on agar, are surrounded by a liquid film, by means of which the bacteria readily accompany the hyphae; the fungi do not grow satisfactorily in the presence of the commonly used bacterial inhibitors; the fungi have temperature and water requirements similar to those of bacteria. Each of these conditions adds to the difficulty of isolation by the common method of repeated transfer, since the hyphae invariably are accompanied by adhering bacteria.

The methods which have been employed in obtaining pure cultures of the Saprolegniaceae were ably reviewed by Kauffman (**4**). These methods as well as those more recently developed not only for the Saprolegniaceae but also for other fungi, may be roughly classified as either mechanical or chemical.

The mechanical methods as advocated by Klebs (**5**), Horn (**2**), Kauffman (**4**), Pieters (**9**) and others, place the mixed culture of

[1] Contribution No. 139 from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University.

the fungus and bacteria on a semisolid culture medium and then repeatedly transfer to a fresh medium the more or less bacteria-free marginal regions of growth until a pure culture is obtained. The following modifications of this general method have been used. Since the temperature ranges of growth for the Saprolegniaceae are usually below those for bacteria, the growth of the bacteria is inhibited more than that of the fungus by holding the contaminated plates at relatively low temperatures. If, in addition to lowering the temperature, the plates are held in a vertical position, the liquid surrounding the hyphae drains to the bottom carrying with it the bacteria and leaving the hyphae at the tops of the plates relatively free from bacteria. Very dilute suspensions of zoöspores from well washed sporangia may be smeared or sprayed onto suitable, semisolid media, thereby mechanically separating the zoöspores from the bacteria.

The chemical methods of isolation employ the principle of growing the contaminated culture on a medium which favors the growth of the fungus but inhibits the growth of the bacteria. In order to obtain such a medium, antiseptics are added to the standard culture media in low concentrations. Boric and salicylic acids were used by Maurizio (**7**), chlorine by Lafar (**6**), and chloride of lime by Melin (**8**).

General experience has shown, however, that the attainment of pure cultures of *Saprolegnia* by the foregoing methods is a laborious, difficult process, and not always successful. The junior author, following the accepted procedure of washing the original material in several changes of distilled water and then repeatedly transferring from the margin of the colony, has sometimes failed to obtain successful isolations. The same lack of success frequently attends modifications of this procedure.

The fungus, though evident in the original material, may fail to appear on artificial media because the growth is completely inhibited by the more rapidly developing bacteria. There is need, therefore, for some method that will simply but effectively achieve isolation by means of inhibiting the bacteria and yet permitting the fungus to grow naturally.

A modified chemical method by which this differential inhibition might be obtained was suggested by some work of Blank and Ar-

nold (1). This work showed that ultra-violet irradiation (2537 Å) of culture media containing carbohydrates so alters the media that they will no longer support the growth of *B. subtilis*. Unpublished work has shown that the growth of other bacteria and common molds can be similarly inhibited. Generally it has been

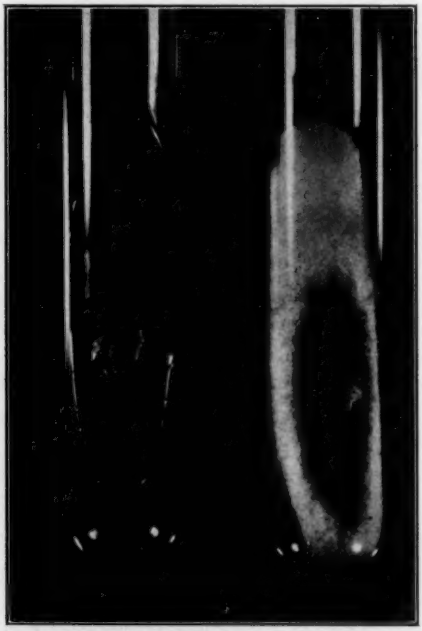

FIG. 1. Potato-dextrose agar cultures obtained from transfers from the 24-hr. growths on non-irradiated medium A (left) and irradiated medium B (right). Note that tube A shows the predominating growth of the bacteria which are completely absent in tube B.

found, however, that a much greater dosage has been required to inhibit the growth of fungi than is necessary to inhibit the growth of bacteria. Thus it would seem that the medium and dosage probably could be so regulated that when mixed cultures of fungus and bacteria are inoculated on the surface of an irradiated culture medium, the fungus would grow but the bacteria would be inhibited.

With this possibility in mind, a medium composed of 1.0 g. of peptone, 5.0 g. of levulose and 20 g. of agar per liter was prepared, sterilized by autoclaving for 15 minutes at 15 lbs. pressure and then 5.0 ml. quantities aseptically placed in 4.5 cm. sterilized petri dishes. Several of these dishes were held uncovered at 29 cm. from a mercury vapor lamp (manufactured by the Hanovia Chemical and Manufacturing Co.) and irradiated for three hours. The lamp was operated on an arc current of 3.2 amperes with 70 volts across the arc. A photograph of the spectrum of irradiation showed lines at 3125, 3021, 2967, 2920, 2894, 2804, 2652, and 2537 Å. The total intensity of the radiation at the distance of 29 cm. was 6.27 ergs per sq. mm. per second.

Specimens of *Saprolegnia* sp. taken from a dead frog found in a marsh were brought into the laboratory in water taken from the same source. Transfers were made from these specimens directly, without washing, onto the centers of irradiated and non-irradiated dishes of the above medium and allowed to grow at room temperature (approx. 20° C). A good growth of *Saprolegnia* with very little bacterial contamination appeared on the irradiated medium. The non-irradiated medium showed a heavy bacterial development with relatively little growth of *Saprolegnia*. After 24 hours, transfers were made from the edges of each culture and placed on tube slants of potato dextrose agar. Figure 1 shows the growth of these slants after 36 hours incubation at room temperature. Tube A illustrates the development of microörganisms transferred directly from the growth on the non-irradiated medium. Although the fungus was transferred, the bacterial associates grew so rapidly that they completely inhibited the fungus. Tube B is a direct transfer from the growth on the irradiated plate and shows a good growth of the fungus, completely free from bacterial contamination.

In this method, the inhibition of bacteria results from the presence of a growth-inhibiting substance which the irradiation produces by a chemical change of the carbohydrate fraction of the medium. The radiant energy is strongly absorbed at the surface of the medium, but the toxic materials produced there diffuse through the entire volume of the medium. The amount of growth inhibition is dependent upon the final concentration of the toxic

material. The most efficient utilization of available energy is thus obtained when a small volume of medium is placed in such a container as to expose a large surface. This was obtained in the above experiment by the use of only 5.0 ml. of medium in a 4.5 cm. petri dish.

Any of the common carbohydrates may be incorporated into the culture medium, to act as the source of the toxic material. Indeed, inhibition will result if only agar is irradiated. For any specific dosage, however, a maximum concentration of toxic material is obtained when levulose is used. The presence of proteins in the medium probably tends to diminish the inhibitive action and hence their concentration should be held at a minimum. These considerations explain why levulose was used in place of the more commonly used carbohydrates and why the concentration of peptone was held so low.

In addition to the original test described above, other isolations were made from similar *Achlya* and *Saprolegnia* collections. These were taken from decaying organic substrata found in ponds and streams near the laboratory. At times it was necessary to subculture for a second time on irradiated material to secure a pure culture, but in every case successful isolations were attained with considerably less difficulty than would have been involved in any of the more commonly used methods.

This method of isolation is offered in the hope that it will be of general use in obtaining bacteria-free cultures of fungi. Such a method, for example, might have prevented the erroneous identification of *B. coli* as the causative agent of coconut bud-rot (Johnston (**3**)), and made possible much earlier the delayed correct diagnosis of *Phytophthora* as the causal organism of this disease (reviewed by C. M. Tucker (**10**)). This work further suggests that the Dermatophytes might be obtained more easily from clinically positive lesions if the scrapings are cultured first on an irradiated medium. In this manner, the growth of bacteria normally present on the skin would be inhibited and the pathogenic fungus allowed to grow. It is to be expected that certain modifications in the above technique, as regards composition of medium, dosage, etc., will be required if this method is to be successfully used on other organisms.

SUMMARY

Bacteria-free cultures of *Saprolegnia* were readily obtained from badly contaminated sources by first growing the organism on an ultra-violet-irradiated medium containing levulose, peptone and agar. The ease of obtaining bacteria-free cultures by this method depends upon the fact that the irradiation so alters the culture medium that growth of bacteria is greatly inhibited with little or no inhibition of the development of the fungus. It is thought that this method will be applicable to the isolation of other fungi.

The authors wish to acknowledge their indebtedness to Professor William H. Weston Jr. for the helpful suggestions offered during this investigation.

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TWO SPECIES OF PHYSALOSPORA IN ENGLAND

NEIL E. STEVENS

The relationship of the very similar fungi found on rotten apples by Berkeley in England and by Peck in New York and in each case named *Sphaeropsis malorum* has been the subject of much discussion and some controversy.

The writer (**6**) has elsewhere given in detail the reasons for his opinion that they are distinct species most easily distinguished by the size and shape and especially the time of coloring of the pycnospores, also that the most appropriate name for Peck's fungus is *Physalospora obtusa* (Schw.) Cooke and for Berkeley's *Diplodia mutila* (Fries) Mont. The present paper reports the finding in England of the ascogenous stages of both these fungi and the development of the pycnospores in pure culture from ascospores. This is apparently the first time the life history of *D. mutila* has been worked out.

PHYSALOSPORA OBTUSA (SCHW.) COOKE IN ENGLAND

That the ascogenous stage of the fungus long known as *Sphaeropsis malorum* Peck is a species of *Physalospora* was proved in pure cultures more than 20 years ago by Hesler (**3**) and by Shear and Beckwith (**5**). During the past 15 years the writer has grown the pycnospores of this fungus in pure culture from ascospores collected on many hosts in the southeastern United States. While this by no means precludes the possibility that an indistinguishable pycnidial fungus might be produced from a quite different ascomycete it seems to render unwarranted the declaration of Petrak and Sydow (**4**, p. 73–74) regarding this species that " Um weitere Konfusionen zu vermeiden, sei hier noch ausdrücklich betont, dass diese Art in den Entwicklungskreis einer echten Cucurbitariacee, höchstwahrscheinlich zu *Otthia Pyri* Fuckel gehören muss und alle Angaben, welche diesen Pilz mit einer *Melanops*—(*Botryosphaeria*

oder *Physalospora*) Art in Verbindung bringen, grundfalsch sind."

The publication of so positive a statement also seems to make it worth while to record the finding in England of *Physalospora obtusa* (Schw.) Cooke, which is the ascus stage of *Sphaeropsis malorum* Peck.

Several weeks' search in England during the summer of 1930 by Dr. C. L. Shear and the writer resulted in finding only one lot of ascospore material, which produced in pure culture typical pycnidia of *Sphaeropsis malorum* Peck. This was found on hawthorn, probably *Crataegus oxycantha* L., at St. Ives, Hunts. Although there appeared to be no reasonable doubt as to the accuracy of these results it seemed unwise to make a report on the basis of a single specimen, particularly one in which no pycnospores were found on the host. During 1930 they did find, however, three lots of *Diplodia mutila* (Fries) Mont., two on ash (*Fraxinus excelsior* L.) and one on apple (*Pyrus Malus*).

Mr. E. W. Mason, of the Imperial Mycological Institute, knowing of our interest in this group of fungi, sent late in 1934 two small specimens of *Physalospora*, hosts unknown, one of them probably apple, which he had received from the Reverend J. H. Adams, Landulph Rectory, Saltash, Cornwall. As they had been collected nearly a year earlier, the spores did not germinate. The specimens did indicate, however, the vicinity of Saltash as a suitable locality to search for more ascospore material. Several days' collecting in August 1935 resulted in securing, with the assistance of Mr. Adams, several good collections on apple prunings from Landulph Parish and one on hawthorn from the Central Park in Plymouth, England, which showed both pycnospores and ascospores of *P. obtusa*. Single spore cultures of these ascospores produced abundant pycnospores typical of *Sphaeropsis malorum* Peck. The ascospores themselves agreed closely with those found in the United States, except that they may average slightly larger. Certainly there seems no doubt as to the identity of the American and English specimens. The presence of the pycnidial stage of this fungus in England and on the continent of Europe has long been known; indeed, it was distributed under the name *Sphaeropsis*

Mali (West) by Vize in 1888 as number *539* in his Micro-Fungi Britannici.

THE ASCOGENOUS STAGE OF DIPLODIA MUTILA (FRIES) MONT. (SPHAEROPSIS MALORUM BERK.)

The discovery of *Physalospora obtusa* (Schw.) Cooke in England was incidental to a search for the perfect stage of *Sphaeropsis malorum* Berk. This search was wholly unsuccessful in 1930 and would almost certainly have been so in 1935 but for the assistance of Mr. Adams. In addition to the material from hawthorn and apple ascospores of which produced in pure culture pycnospores typical of *S. malorum* Peck, a single specimen of *Physalospora* found on ash and one of those on apple at Saltash proved to have ascospores somewhat larger than any hitherto found in England, and single ascospore cultures made from these produced early in January 1936 pycnospores typical of *Diplodia mutila* (Fries) Mont. (*S. malorum* Berk.).

The differences between the perfect stages of the two fungi here discussed are apparently confined to the size of the ascospores. Those of *Physalospora obtusa* measure 23 to 38 $\mu \times 7$ to 13 μ, mostly 26 to 34 $\mu \times 7$ to 12 μ, while those of the other fungus measure 30 to 39 $\mu \times 12$ to 16 μ, mostly 30 to 36 $\mu \times 13$ to 14 μ. The spore measurements overlap somewhat and on the basis of the perfect stage alone one might well hesitate to consider them distinct species. These differences are more readily observable, however, than the measurements would suggest, for the moment that Mrs. A. F. Kempton, who made all the cultures and who has examined much material of *Physalospora*, saw spores of the fungus on ash she was sure that this was "a different fungus." Moreover, the ascospores of this fungus on ash approach even more closely in size the tropical and subtropical species *P. rhodina* or the northern *P. glandicola* than they do *P. obtusa*. Yet the pycnospores of these two fungi are so very different that no one would consider including either one of them in the same species with the fungus found at Saltash. The accumulating evidence indicates that most of the species of *Physalospora* are more easily recognized in the pycnidial than in the perithecial stages.

Deciding on the proper name for this fungus raises the usual difficulties. It is apparently not *Physalospora Cydoniae* Arnaud, the ascospore size of which is given (**1**) as $23 \times 11\,\mu$. There is, of course, no certainty as to what the pycnidial stage of *P. Cydoniae* might be since Arnaud's suggestion that it is *Sphaeropsis pseudodiplodia* is based merely on association. Nor has the writer thus far been able to find any described species to which the perfect stage of *Diplodia mutila* may with reasonable certainty be referred. It thus appears best to cite it as **Physalospora mutila** (Fries) N. E. Stevens, comb. nov. with the hope that someone will shortly find an older valid name and reduce this to synonymy. Synonyms of the pycnidial stage were given by the writer (**6**, *p. 547*).

Pycnidia simple or compound in black stromata, variable in size up to 2 mm. in diameter. Pycnospores at first one-celled and hyaline with a thick glassy wall, usually remaining in this condition for a long time, some of the spores usually becoming brown and septate; 20 to $27\,\mu \times 10$ to $16\,\mu$, mostly 25 to $27\,\mu \times 10$ to $12\,\mu$. Perithecia in stromata similar to the pycnidial or in the same ones. Paraphyses numerous, branched, interwoven, and apparently anastomosing, as in all fungi of this genus. Asci regularly eight-spored. Ascospores hyaline and nonseptate, a few later becoming two-septate; 30 to $39\,\mu \times 12$ to $16\,\mu$, mostly 30 to $36\,\mu \times 13$ to $14\,\mu$.

This fungus differs from *Physalospora obtusa* chiefly in the larger size of the ascospores, and the size, appearance and time of coloring of the pycnospores. Type specimen on cut stick of *Fraxinus excelsior* L. at Saltash, Cornwall, England.

ANOTHER PYCNIDIAL FUNGUS (DIPLODIA SARMENTORUM FRIES) ON THE SAME HOSTS

The folly of attempting to decide matters of life history in this group of fungi on the basis of association on the host was again illustrated by the studies of the material from England. On the ash stick which bore the ascospores from which *Diplodia mutila* was produced in culture were found a few pycnidia containing pycnospores of this species. Much more common and abundant, however, and closely associated with the fungus in question were pycnidia very similar in size and general appearance but containing

spores which almost uniformly become brown before they are discharged from the pycnidium. These spores are usually one-septate and many of them are constricted at the septum. They are also somewhat smaller in size than the pycnospores of either of the other fungi discussed above. While some spores as long as 26 μ are noted, in by far the largest number of specimens measured the spores were about 18 to 23 μ in length by 8.5 to 10 μ in width. This fungus was found on apple and hawthorn as well as ash, and careful comparison of it with *D. mutila* on the various hosts as well as in pure culture at various temperatures leaves no doubt that the two are distinct.

In attempting to select a name for this fungus, slides of numerous type and authentic specimens prepared during the past 15 years were re-examined. As will be evident from the partial synonymy given below, this fungus has been described under a variety of names, the oldest of which and the one which will be adopted here is *Diplodia sarmentorum* Fries. This species was described by Fries as *Sphaeria sarmentorum* in 1818 (**2**, *p. 107*) from material on *Menispermum canadense* in the Botanical Garden at Lund, Sweden. In his Systema Mycologicum, 1821, the species is listed with a description under the same name. In his Summa Vegetibilium he transferred the species to the genus *Diplodia* (page 417), at the same time indicating that he considered it identical with *D. mamillana*, which, however, proves on examination to be a quite different fungus. The fungus was distributed in his Scleromyceti Sueciae as No. 18 [not 28, as it is sometimes listed because of a defective type in the label].

There are three good specimens of this number in the Mycological Herbarium of the Bureau of Plant Industry, U. S. Department of Agriculture, one in the original set, one in the so-called Sbarbaro collection, and one in the Michener Herbarium. They are all alike and all show good spores. The packet in the Sbarbaro collection bears this comment in Fries' handwriting: "*Diplodia mamillana-sarmentorum* Fries Summa p. 417."

DISTRIBUTION OF DIPLODIA SARMENTORUM

Like *Diplodia mutila, D. sarmentorum* is relatively rare in the continental United States. Thus far the writer has seen only six

specimens, of which four, including the one described by Peck as *Diplodia Alni-rubrae*, were from the same region in which *D. mutila* is most commonly found, that is, the Northwestern States. Peck's specimen was collected on *Alnus rubra* at Rollingbay, Wash., by E. Bartholomew. The other specimens were on apple or pear from western Oregon.

Diplodia sarmentorum, however, appears to be common in Europe. The list of synonyms gives some idea of its distribution and host range. The writer has studied this species in cultures made from material collected by Fragoso at Madrid, Spain, in 1922 on *Alnus cordifolia, Genista tinctoria, Pyrus eleagnifolia*, and *Viburnum rugosum*, and on cultivated *Citrus* (both lemon and orange) and walnut bark from Acireale, Sicily, 1930 by Fawcett. The writer collected it in England on hawthorn and cultivated apple in both 1930 and 1935. On the whole, however, fungi of this group are by no means as plentiful in England as in the eastern United States. At least one important factor may be the scarcity of favorable substrata. As pointed out many years ago by Tulasne, these fungi are commonest on branches that have been cut from healthy trees and left for a period on the ground. Such prunings are abundant in the eastern United States but relatively rare in England, where prunings from fruit trees are usually burned and where there is very little indiscriminate cutting of healthy woody shoots.

DIPLODIA SARMENTORUM Fries, Summa Veg. 417. 1849.

Synonyms based on examination of type or authentic specimens.

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Diplodia salicina Lév. Ann. Sci. Nat. III. **5**: 292. 1846.
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Diplodia Siliquastri West. Bull. Soc. Roy. Bot. Belg. 244. 1863.
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Diplodia Rosae West. Herb. Crypt. fasc. 25, No. 1227. 1859. Kickx, J. Flore Crypt. Fland. **1**: 395. 1867.

Diplodia Euonymi West. Herb. Crypt. fasc. 19, No. 930. 1854. Kickx, J. Flore Crypt. Fland. **1**: 395. 1867.
Diplodia inquinans West. Herb. Crypt. fasc. 8, No. 371. 1849. Kickx, J. Flore Crypt. Fland. **1**: 398. 1867.
Diplodia Crataegi Fuckel, Symb. Myc. 393. 1869.
Diplodia Coryli Fuckel, Symb. Myc. 393. 1869.
Diplodia Humuli Fuckel, Symb. Myc. 393. 1869.
Diplodia Tiliae Fuckel, Symb. Myc. 394. 1869.
Diplodia malorum Fuckel, Symb. Myc. 395. 1869.
Diplodia Alni Fuckel, Symb. Myc. 395. 1869.
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UNIFORMITY AND STABILITY OF MYCOLOGICAL NOMENCLATURE[1]

C. L. Shear

We are sometimes inclined to become discouraged on account of the lack of progress being made in settling our nomenclatorial difficulties. We found some encouragement, however, in the fact that the mycologists of the 6th International Botanical Congress chose this subject for discussion; as it indicated that systematic mycologists of all countries were recognizing the fact that the conditions and problems met with in the nomenclature of the fungi are very different and much more complex than those met among the flowering plants, and therefore need special consideration. If uniformity and stability in the use of the names of fungi are to be attained, these differences must be recognized and plans formulated to meet the different conditions and problems.

So far as I am aware, no one denies at present the desirability of securing greater uniformity and stability for the generic and specific names of fungi, in so far as this is compatible with the true aims and purposes of systematic mycology.

The fundamental requirements of a satisfactory nomenclature are uniformity, stability, exact application, and convenience.

Before any successful plan for accomplishing these purposes can be made, however, we must have a full knowledge of the conditions and problems which confront us—and in order to understand these we must know the history, evolution, and course of development of the names and concepts prevailing at the present time.

The founding of genera and species of fungi in a broad application of these terms may, I think, be properly attributed to Micheli (7) who might be termed the "Father of Mycology." Some of our present generic names are still quite appropriately credited to

[1] Paper presented by invitation at the 6th International Botanical Congress, Amsterdam, Holland, Sept. 5th, 1935.

him. As to specific names, however, the polynomials used by him and his successors until the time of Linneaus, and even later by Haller and others, were entirely impracticable for general purposes and had to be abandoned.

The development of a true concept of genera and species of fungi as natural groups was necessarily slow on account of the lack of methods and facilities for obtaining exact knowledge of such plants. With the development of the microscope and an increase in the number of students, more definite knowledge was obtained in regard to the characters and general limitations of genera and species. Progress, however, was slow, and even at the time of the publication of Fries' Systema (**4**), 1821–1832, which the priorists regard as the best starting point for most of the fungi, the so-called genera were mostly not natural divisions, but heterogeneous groups of species of very different generic affiliations. The lack of exact knowledge of these plants, especially the micro-fungi, on account of their small size and pleomorphic life histories, has made the segregation and definition of natural groups a very slow and difficult process; so that even today there are great numbers of genera and species named whose exact definition and limitation are impossible. Under such conditions it should be evident that it is extremely difficult to say just when any particular generic or specific name was validly published, and real priority established. According to the 1930 International Rules, Sec. 3, Art. 19: "A name of a taxonomic group has no status under the Rules and has no claim to recognition by botanists, unless it is validly published." Unfortunately, the Rules do not give a very good positive definition of valid publication, but Art. 37 (2) says: "A name is not validly published unless accompanied by a description of a group or by a reference to a previously and effectively published description of it.

Under rejection of names, Sect. 12, there are three articles, 62, 63, and 64, under any of which many of our old fungous names become invalid. Art. 62 says: "A name of a taxonomic group must be rejected if, owing to its use with different meanings, it becomes a permanent source of confusion or error." Art. 63 says: "A name of a taxonomic group must be rejected when its application is uncertain." And Art. 64 reads: "A name of a

taxonomic group must be rejected if the characters of that group were derived from two or more entirely discordant elements."

It seems clear from these quotations that a great many of our best known fungous names are invalid as originally proposed. Thus we must decide whether to discard all the names of genera and species insufficiently described and including heterogeneous groups or validate them at the time they were first satisfactorily described and segregated. In either case the difficulties are so great that no uniform or satisfactory decisions could be made on a priority basis and the result would be more change and confusion of names instead of stability.

In order to emphasize this difficulty more clearly and forcibly, it may be well to call attention to a few specific cases which are more or less typical of hundreds of others. Take, for example, the genus *Dothidea*. The name was first published by Fries (2) in 1818, with the following description:

"DOTHIDEA, Fr.

"Tab. V. f. 4, 5.

"*Receptaculum* nullum. *Perithecia* difformia, tuberculoso-corrugata, intus solida, humectata mulliuscula, *ostiolo* nullo."

Brief diagnoses of five species are added. The first, *D. conspersa* (Tode), according to Rehm, is *Tympanus conspersa* Fries; but Fries did not regard this as typical of the genus as he adds: "Heteroclita species." Most of the other species are doubtful and none is to be found in *Dothidea* as now applied.

The next year, 1819, Fries (3, p. 87) redescribed the genus and included seven species and two varieties, discarding two from his previous list and adding four, thus complicating rather than clarifying the situation. His next treatment of it was in 1823 (4, vol. 2: 548–65). Here he enlarged the genus still further, referring to it 54 species separated into four divisions. Among the species in this heterogeneous collection were plants which at present are scattered through a dozen or more different genera belonging to different families of Discomycetes, Pyrenomycetes and Imperfecti. Could one by any stretch of the imagination at present regard this *omnium-gatherum* as a genus? Our late French colleague, Che-

nantais, would have called it " un gâchis," which in colloquial English would be a " mess " or " Mischgattung " of German mycologists.

Again, in 1825, Fries (**5**, p. 112) treats *Dothidea*, modifying his previous descriptions somewhat but mentioning no species; simply citing " Syst. Myc. **2**: 548," and remarking that the genus is natural but very difficult to define. His next and last treatment in 1849 is confined to a catalogue of Scandinavian species (**6**, p. 386) including 24 as genuine members and 4 as uncertain. He begins the list with the section " erumpentes " and names first *D. ribesia, D. Berberidis* and *D. Sambuci*. The inclusion of these three species, one of which, *D. Berberidis*, he had not before put in the genus, and their position at the head of the list, is apparently due to the work of DeNotaris eight years earlier.

Little was known about the microscopic characters of any of these plants, especially the asci and spores until DeNotaris (**8**, p. 65) gave a detailed description and good illustrations of *D. Sambuci* var. *Hederae* and *D. Berberidis*. In 1849, in the same series of papers, he described and illustrated in detail *D. ribesia* and stated that previous descriptions of this species by Nees, Chevalier, and Rebentish were very incomplete and unsatisfactory. He says the genuine species of *Dothidea* are the three just mentioned, and the others included by Fries should be excluded so far as he had been able to examine them.

Here I think we may say that the genus *Dothidea* was first really established or " validly published " according to the Rules. The three species referred to above were included in it by nearly all subsequent authors, including Tulasne, who gives a detailed description with illustrations of the life history of *D. ribesia*.

Winter in 1887 restricted the application of the name chiefly to the species mentioned by DeNotaris, including hyaline as well as colored ascospores. In the meantime many of the species of Fries had been transferred to other genera. Saccardo (**9**) took *D. Sambuci* which has colored spores as his first species and referred *ribesia* and *Berberidis* to *Plowrightia*, because he believed the spores in those species to be hyaline or only slightly greenish. Whether there are any real generic differences between *D. ribesia* and *D. Sambuci* remains to be determined by further studies of their life

histories and conidial stages. The general usage of mycologists throughout the world since DeNotaris has been to regard *D. Sambuci,* at least, as a typical member of this genus.

In 1915, Theissen and Sydow (**18**, p. 328) discussed the genus, pointing out what a very heterogeneous group of species Fries had included, and decided to select as the type *D. moriformis* (Ach.) Fries, the first species mentioned by Fries in 1823. Since the identity of this species is doubtful and since so many species had been added to the genus which were not congeneric with *D. Sambuci,* they decided that the name *Dothidea* should be discarded entirely, and the group typified by *D. Sambuci* should have a new name, *Systremma,* and *D. ribesia* and *D. Berberidis* should be put in *Dothidella.* Thus an attempt to follow the rules as they stood at that time results in the proposal to discard one of the oldest and best known generic names among the Dothidiales and the one on which both the family and order were based, because the first species listed by Fries in the place cited happened to be uncertain. Clements and Shear (**1**) in 1931, selected *D. Sambuci* as the type of this genus, in accordance with the recommendation of the Cambridge revision of the International Code, which would permanently establish it in the sense in which it has been generally used for nearly one hundred years.

The history of *Dothidea* in its general aspects is very similar to that of hundreds of generic names found among the Ascomycetes as well as other groups. A few other changes of names which would be required on a priority basis are as follows:

Amphisphaeria Ces. & DeNot. 1863 would become *Sphaeropsis* Lév. 1842

Cordyceps Fries 1849 would become *Corynesphaera* Dumort. 1822

Daldinia Ces. & DeNot. 1863 would become *Peripherostoma* Gray 1821

Linospora Fuckel 1869 would become *Phoma* Fries 1823

Nectria Fries 1825 would become *Hydropisphaera* Dumort. 1822

Valsa Fries 1825 would become *Syphosphaera* Dumort. 1822.

In discussions of some of these names in earlier publications (**1**, **2**, **4**, **7**) we have given different synonyms for some of them as Linnaeus instead of Fries was taken as the starting point. What the synonymy would be and what changes would be required by the application of the priority rules in the case of genera containing heterogeneous species depends chiefly on the choice of the type or standard species for each genus. It would seem clear from the case of *Dothidea* just described that the selection of the type of a genus is of far greater importance in preserving our old and well established names and insuring their stability, than the question of priority of publication. It would also seem self-evident that the method followed by Theissen and Sydow in the case just described will not give us the stability and uniformity of names, which has been the avowed purpose of all laws, codes, and rules since the first Botanical Congress in Paris in 1867. The plan to fix names according to priority or according to typification based on the first species described or mentioned can only bring about great change and confusion in the use of names and serve no useful purpose. As to priority, how can one determine when a genus such as *Dothidea* was really validly established? The early descriptions were not sufficiently detailed or accurate to make identification possible and the species included were also frequently very doubtful. As a matter of fact, in the case of *Dothidea,* the genus was not really established until DeNotaris gave his detailed description and illustrations; so one might claim that he was the real author of the genus. This shows how impracticable either of the proposed plans, priority of publication or typification by first species, is; if we regard the chief aim and purpose of rules to be the attainment of uniformity and stability in the use of names with the least change and inconvenience possible. It would therefore seem clear that generic names must be fixed on a type basis selecting such types as will fix names according to their present usage so far as possible.

The most important need at present, therefore, is the adoption of a practical plan to preserve our present names and give them a definite and fixed status within a reasonable period of time. The writer believes such a plan is available. The phanerogamic botanists have attempted to establish names on the basis of priority

of publication, realizing that the plan would bring about many changes in current usage, but hoping eventually to secure stability. Ethical considerations have also been urged in support of the priority plan; it being contended that great injustice would be done to the oldest author of a plant name if his name were not adopted and he given credit for it. While we believe that proper credit is due the early botanists who made important contributions to systematic botany, yet abundant recognition and honor can be bestowed upon the deserving without entailing so much trouble and inconvenience to the great number of people who today have to use technical plant names, as the application of the priority rule would entail. It would seem to be much more in harmony with high ideals of justice and ethics to credit the authors who first adequately described, illustrated, and preserved specimens of the plants named. Past experience has already demonstrated the impracticability of the priority method to attain the desired end, even with the flowering plants. As for fungous names, we should be very thankful that no general attempt has yet been made to apply the priority plan, as very few of our most familiar names would have been left. For further discussion of this phase of the subject we would refer to previous papers by the writer which are listed at the end.

Before there can be any stability of generic names, however, those applied to genera containing two or more heterogeneous species must be fixed to some particular species which shall be held as the nomenclatorial type or standard species. The type method of fixing generic and specific names was proposed by American botanists in their efforts to fix the application of such names. This plan offers the simplest and most practical method of definitely fixing the application of a generic name to at least one species which shall be the basis for the generic description and concept, and about which other con-generic species may be grouped.

Owing to a lack of understanding of the conditions involved and the results which would follow, the first plans for selecting types were unfortunate. The selection of the first species listed under a genus seemed very simple and easy of application; but

when applied to heterogeneous genera frequently resulted in the application of a name to a group entirely different from that to which it is now generally applied. The case of *Dothidea* which we have described is an excellent example. It was next suggested that many of the unfortunate changes which would be caused by the first species plan would be avoided by selecting the best known or an economic species, if such happened to be included in the original list. This was a great improvement so far as the flowering plants were concerned, but does not meet the needs of mycology. Fortunately, the recommendation for selecting types of genera of non-vascular cryptogams, as adopted in the 1930 rules of the International Congress at Cambridge, if followed, will make it possible to fix our present generic names of fungi in such manner as to reduce further changes of names and their application to a minimum. The recommendation is as follows:

Section 2, Art. 18, Recommendation 6: "In selecting a nomenclatorial type of a genus of non-vascular Cryptogams, botanists should, where possible, choose a species that will fix the generic name as it is now commonly applied."

Article 5 covers this in a more general way "In the absence of a relevant rule or where the consequences of rules are doubtful, established custom must be followed."

An attempt to carry out this plan was made by Clements and Shear (1) in 1931. It is perhaps needless to say that many unfortunate choices of types were made. These may be easily changed. The practicability of the plan, however, was demonstrated. What is now needed is the appointment of a standing committee of international systematic mycologists most familiar with the nomenclature of the major groups of fungi and who are in sympathy with this plan, to prepare a list of accepted genera typified according to the method recommended in the code as already cited.

By the above method of selecting types of genera, supplemented when necessary by resort to the list of *nomena conservanda,* it will be possible to preserve practically all of the names at present in common use except for such changes as may be necessitated by revision of generic concepts and limitations due to lack of knowl-

edge of the species and their relationships and to differences of opinion of monographers.

To summarize briefly: To stabilize present generic and specific names and definitely fix their application are the greatest needs of systematic mycology.

Generic definitions and concepts among the fungi have developed gradually as our knowledge has increased and though a generic name may have been proposed at an early date in many cases no adequate generic description or concept was attached to it until a much later date, making it very difficult to say at what date it was "validly published."

It has been demonstrated that stability and uniformity can not be attained by the application of the priority of publication plan, but can be accomplished to a great degree by the selection of such type species and specimens as will fix the names as they are generally applied at present.

The subject has been further discussed in a previous series of papers cited (1: p. 14–15, 10–17) in the bibliography appended.

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BASIDIAL PROLIFERATION THROUGH CLAMP-FORMATION IN A NEW SEBACINA [1]

DONALD P. ROGERS [2]

(WITH 34 FIGURES)

The classical studies of the clamp-connections of basidiomycete hyphae by Kniep (**10**) and Bensaude (**1**) and the recent illuminating discussion by Martens (**12**) provide an essentially complete basis in observation and hypothesis for the interpretation of these structures. The cytological phenomena involved in the formation of the clamp-cell were first described by Kniep; and upon a comparison of the clamp as he had observed it with the crozier of *Pyronema* as described by Claussen (**4**) he established the homology of the two structures. Bensaude, whose single-spore cultures of hymenomycetes demonstrated the genetical dissimilarity between the nuclei whose conjugate division is associated with clamp-formation, discovered the actual functional significance of the clamp: that is, it is an organ insuring that each of the hyphal cells between which it lies shall possess not sister nuclei, but a dikaryon of complementary members, one nucleus being descended from either member of the parent dikaryon. Martens undertook to push the phylogenetic problem back to the rise of the crozier. He pointed out that even in crozier-bearing species of Ascomycetes conjugate division occurs within the basal, broader portions of the ascogenous system without formation of such a special structure, croziers usually being present only where the hyphae are too narrow to contain two nuclei, or two spindles, placed side by side.[3] In a primitive form in which the crozier had not yet been evolved, he pointed out, simultaneous division of paired nuclei in such a narrow portion of the ascogenous

[1] Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, no. *142*.

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[3] Cf. Martens (**12**), pp. 270–273, and especially footnote 1, p. 273.

system would take place with the spindles lying longitudinally and one above the other, and would result in the formation of a series composed of two sister nuclei lying above two sister nuclei. Only the second and third nuclei of such a series would be adjacent and complementary, and this median pair would subsequently be walled off together, by septa formed across the mitotic spindles, leaving the basal and apical nuclei isolated.[4] Asymmetric growth of the median cell as it enlarged to form an ascus might well, however, thrust the uninucleate apical cell aside, to the degree that fusion with the basal cell could take place; such fusion would be the expected result of the mutual affinity of the isolated nuclei. Thus a crozier would be completed. Martens finally maintained that by precocity in membrane development the curvature which primitively occurred *after* conjugate division came to occur before[5]; and that by extension of this tendency in membrane development apical elongation of the hypha beyond the region of recurvature similarly took place before division, bringing about the lateral origin of the clamp-beak of basidiomycete hyphae. It may be noted that such ontogenetic anticipation, such development of a cell-membrane in advance of the nuclear development which makes it appropriate, is not unknown elsewhere; as an example, epibasidia often are budded out by the hypobasidium before division of the diploid nucleus, or after its first division, in *Tulasnella* and in various genera of the Tremellaceae.[6] By this hypothesis, which rests on familiar processes, Martens gave causal intelligibility to a course of development previously only teliologically comprehensible. The theoretic interpretation thus completed is nevertheless based, so far

[4] "This is exactly the arrangement encountered by Guillermond (Ann. Myc. **3**: 347, *fig. 86–91*) in *Peziza Catinus*."—Martens.

[5] In *Humaria rutilans*, according to Gwynne-Vaughan (**7**), curvature may occur either before or after conjugate division. The croziers of this species (**7**, fig. 8–11) are figured as being less specialized, more clearly representing recurved hyphae, than those of *Pyronema*, and may well be taken to exemplify the earliest stage in the evolutionary process described by Martens. The figures may, however, represent only the recurved ends of the early ascogenous processes (Gwynne-Vaughan & Williamson (**9**), p. 363, and fig. 31–35, 37–39; Claussen (**4**), fig. 35–39, 54, 55), which are not, according to these authors and the observations of the writer, definitive croziers, but structures giving rise to croziers.

[6] Rogers (**15**), p. 92, *fig. 5, 20–22;* Whelden (**18**), p. 423; (**19**), p. 52; (**20**), p. 509; (**21**), p. 125.

as the Basidiomycetes are concerned, on study of the clamp-connection only as a component of the hyphal system.

In his detailed consideration of the ascogenous hyphae of *Pyronema,* Claussen wrote: "As a result of the development of croziers and the accompanying nuclear- and cell-divisions, two nuclei of unlike sex always remain in reserve in stalk and beak for the formation of additional asci." Primarily, just this is the result accomplished by the crozier, however the course of its development be regarded: whether it be interpreted teliologically, as a single process—which it assuredly now is—or more rationally, as a series of processes, the curvature and fusion being taken to be "purely corrective" (**12**) of a division after which one of each pair of daughter nuclei has been left isolated. Conceivably the Ascomycetes are descended from ancestors in which karyogamy was invariably followed by meiosis and spore formation (cf. Darlington (**6**)); in any event, all developments beyond the simplest imaginable ascogenous system, either through increase in number of nuclei or through complexity of branching, may be taken to be associated with augmentation of the number of asci resulting from a single cytogamy; Claussen's phrase "remain in reserve for the formation of additional asci" is thus justified. Furthermore, Claussen's dictum as to the function of the crozier, like Martens's hypothesis as to its origin, is applicable whether or not in any particular form the paired nuclei can be shown to be genetically different. It seems likely that primitively complementary pairs were present, as they surely now are in some forms (e.g., *Neurospora tetrasperma* (**5**)), although in homothallic species this need not be the case; nor would the paired nuclei be sexually differentiated if they were already diploid. But Gwynne-Vaughan & Williamson have pointed out (**9**, pp. 363, 364) that the observed arrangement of nuclei in the crozier could be brought about by a tendency to form septa across the spindles of the conjugately dividing nuclei. By this means a single nucleus would be isolated in the beak and another in the stalk quite as well as by association of a median complementary pair. And since two nuclei from the ascogenous hyphae, be they haploid or diploid, are necessary to the formation of one ascus, the "reserve" must still be of biological advantage to the organism.

The operation of the crozier-mechanism in the multiplication of dikaryons is then, both from observation and by hypothesis, connected primarily with the multiplication of gonotoconts. If the clamp be the homologue of the crozier, as on the hypothesis already summarized, then it is to be inferred that the clamp may similarly be associated with the multiplication of gonotoconts. That such is actually the case has been mentioned by Kniep (**10**, p. 392) and Bensaude (**1**, p. 121). Such association of the clamp-apparatus with basidial proliferation is reported by Brefeld (**2**) in *Phleogena* (*Pilacre Petersii*) and by Kniep (**10**) in what is probably *Corticium coronilla* (*C. varians* Kniep), in *Hypholoma fasciculare*, and in *Agaricus* sp. According to the writer's observations it occurs also in *Tulasnella rutilans*, in *Gloeotulasnella traumatica*, in *Mylittopsis Langloisii* of the Auriculariaceae, and in *Peniophora aurantiaca;* it is unquestionably discoverable by special search in many other fungi. Thus far, however, no study of this aspect of the clamp mechanism has appeared. In view of the fact that such objection to the homology of clamp and crozier as appears seems to arise in part out of a rather hazy general notion that the crozier is a " reproductive " structure while the clamp is " vegetative," such a study appears to be desirable.

Living material of a fungus in which in the hymenium the clamp serves exclusively and conspicuously in the direct proliferation of basidia recently came to hand; the present account is based on study of this material. The fungus being an undescribed species, a diagnosis of it is first presented.

DESCRIPTION OF SPECIES

Sebacina prolifera sp. nov.[7]

Fructification effused, very thin, when fresh mucous-gelatinous, hyaline, when dry nearly or quite evanescent, perceptible only under the lens, as an interrupted colorless varnish-like incrustation;

[7] Fructificatio resupinata, mucoso-gelatinosa, tenuissima, hyalina, sicca evanida; hyphae laxe intertextae, conglutinatae, nodoso-septatae, 1.5–2.5 μ diametro; basidia in cellula clavata gesta, per ansam anastomosis basalem prolifera, primum globosa, maturitate pyriformia vel oblonga, cruciato-septata, 10–14 × 8–9 μ, epibasidia 4 crassa, 2–3 μ diam., usque ad 20 μ longitudine, ferentia; sporae subcylindraceae, utrinque leviter attenuatae, arcuatae, 18–20 × 3.5–4 μ, per repetitionem germinantes.

in section 15–60 μ thick, composed of an ill-defined subicular layer of interwoven hyphae, thin-walled, 1.5–2.5 μ thick, with clamps at all septa, embedded in a gelatinous matrix, and supporting a fairly even hymenium; basidia borne on erect stalks slender at the base and expanded at the basidium, with stalk and basidium connected by a large clamp, trumpet-shaped, broadened apically, on which is borne a second basidium; probasidia subglobose, becoming elongate; hypobasidia oblong to pyriform, 10–14 $\times$8–9 μ, cruciate-septate, bearing 4 epibasidia 2–3 μ thick, up to 20 μ long; spores subcylindric, slightly attenuated at either end, blunt, curved, 18–20 $\times$ 3.5–4 μ, germinating by repetition.

On lower side of a sodden, well-rotted, decorticate log of *Ulmus* sp., lying on the ground, Linder's Woods, Iowa City, Iowa, III. 20. 1935, *D. P. Rogers 80,* type. Type deposited in the author's herbarium, the mycological herbarium of the University of Iowa, the Farlow Herbarium, the U. S. National Herbarium, and the herbarium of the Royal Botanic Gardens at Kew.

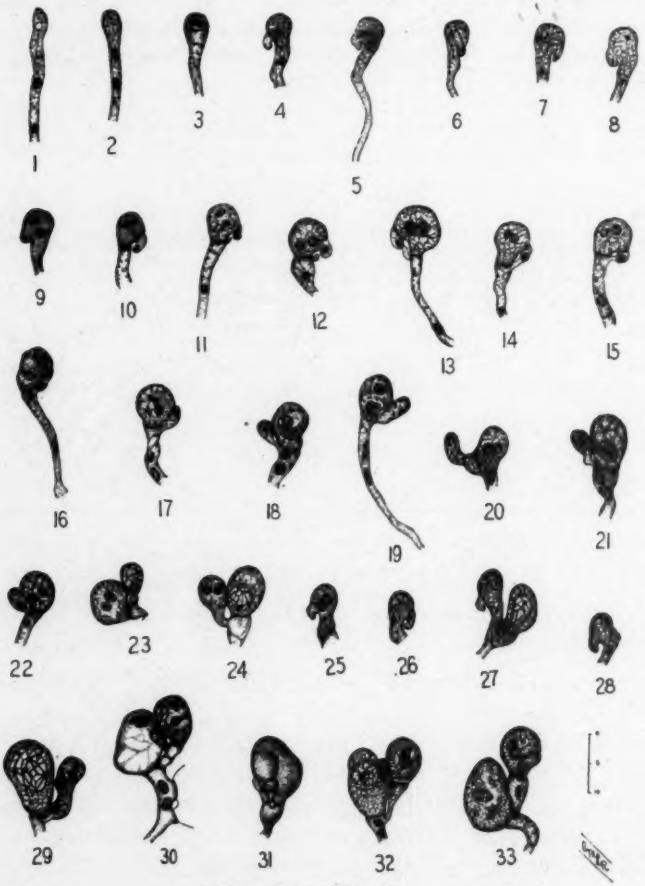
S. prolifera belongs among the delicate gelatinous members of the genus, near *S. fugacissima* and *S. calospora.* It differs from all species of *Sebacina* known to the author in the broadened subbasidial cell and the trumpet-shaped clamp by which basidia proliferate, and also by the slender-cylindric, blunt spores. In the latter character it somewhat resembles *S. calospora,* where the spores are, however, more slender and more attenuate.

METHODS

For preliminary examination of *Sebacina prolifera,* material was crushed beneath the cover-slip in a solution of KOH and phloxine, as recommended by Martin (**13**); the taxonomic description was drawn up from such preparations. More critical examination appearing desirable, portions of the fruiting-layer adhering to flakes of the substratum were fixed in Flemming's weaker solution and embedded in paraffin. Of this material sections were cut at 12, 5, and 3 μ, stained in iron-alum haematoxylin, destained in picric acid, and counterstained in phloxine. Only in the 12 μ sections were the relations of the various hymenial elements favorably shown; the account that follows was drawn from study of such preparations.

OBSERVATIONS

The thin basal layer of the fructification of *S. prolifera* is made up of slender clamp-bearing hyphae, loosely interwoven, running



FIGS. 1–33. *Sebacina.*

along the substratum or diagonally away from it, and held together by a gelatinous matrix. From these subicular hyphae arise perpendicular branches, of somewhat greater diameter, which become distally clavate as they approach the surface of the hymenium. A

branch of this sort, the primordium from which a basidium and its stalk are to be differentiated, is usually without septa and contains a single dikaryon which lags considerably behind the apex of the cell (FIG. 1). With further growth the primordium becomes abruptly expanded near the tip and the nuclei move to a subapical position (FIG. 2, 3). From one side of the inflated end, just below the widest part, is put out a sharply recurved beak; at the same time the end swells out laterally so as to lie about equally beyond beak and stalk (FIG. 4). Subsequently one nucleus migrates to a position above the base of the beak (FIG. 5). The nuclei now undergo conjugate division, the one spindle lying partly in the beak, the other well against the opposite wall (FIG. 6). The basal daughter nucleus of this second division-figure immediately moves down into the stalk (FIG. 7, 8); nuclear reorganization takes place apparently almost at once (FIG. 9), and septa are formed separating from stalk and beak the young basidium with its dikaryon (FIG. 10).

The completion of the clamp clearly is brought about essentially as Buller (3) has described it in various hyphae, by "hook-to-peg," and not hook-to-side, fusion. The stalk puts out from just below its distal cross-wall a short, very slender outgrowth (FIG. 11–12), which comes in contact with the comparatively passive tip of the beak and fuses with it, the lumina becoming continuous (FIG. 13, 14), and the beak nucleus moving into the stalk (FIG. 15, 16). If the young basidium has enlarged little beyond its condition at the time of formation of the beak, the clamp-cell may be all but appressed to the wall of the basidium (FIG. 11, 14); if considerable growth has meanwhile occurred, the outgrowth from the stalk may become conspicuously peg-like before reaching the beak (FIG. 12, 13). After completion of the clamp the nuclei from stalk and beak come to lie together some distance from the apical end of the cell (FIG. 17).

The primordium has at this stage developed into a long stalk, tubular at the base, considerably broadened at the summit, a more or less globoid probasidium, and a connecting clamp, very slender at the base, flaring towards its union with the basidium (FIG. 17). Further development of the stalk-cell dikaryon is not perceptibly coördinated with the nuclear or morphologic development of the

basidium. The apical, outer wall of the clamp, usually close beside the probasidium, commences to swell so that the enlargement soon involves the whole upper part of what was the beak (FIG. 18). Enlargement may be about the same in all directions, and result in a globoid body lying close against the basidium (FIG. 21, 22), or apical elongation may occur, so that a clavate appendage appears, seated on the clamp (FIG. 19, 20). After the swelling is well under way, the nuclei of the stalk move through the clamp into the swollen portion (FIG. 22, 23), and a structure is formed beside the already differentiated probasidium (FIG. 24) essentially the same as an early stage of the primordium (FIG. 3).

In this secondary primordium the entire process occurring in the primary is repeated—pushing out of a beak, conjugate division, cutting off of the binucleate probasidium, fusion of beak and (secondary) stalk, reconstitution of a dikaryon from beak and stalk nuclei (FIG. 25–30); the stages are so far identical that it is frequently difficult or impossible, because of loss of basal attachments in sectioning, to determine whether structures observed belong to primary or later clamps. The stalk of the second basidium is continuous with that of the first, and the basally migrating dikaryon moves far down in the primary stalk (FIG. 30). After a varying interval the second clamp develops a third basidium and stalk (FIG. 31–33); and so on: groups of four or five basidia, each formed from the clamp of the next larger, are frequently intact in 12 μ sections, and even as many as six or seven have been observed (FIG. 34 *a*), the oldest so far disintegrated as to be scarcely perceptible. There is reason to suppose, from the thickness of the hymenial layer in some parts, that even larger numbers of basidia are produced upon a single fertile hypha. All principal stages in the growth of the basidia occur in the preparations examined. Since they agree in all essential points with the course of development already established for the tremellaceous basidium, description here is superfluous.

DISCUSSION

The clamp mechanism here described may well be compared, as was the hyphal clamp, in the work of Kniep and Bensaude, with the similar mechanism of the most completely known ascomy-

cete diplophase, that of *Pyronema confluens*. It is shown by Claussen's observations that a clamp—that is to say, a completed crozier—once having been formed, there are two ways in which the cells which it unites may continue the multiplication of cells and dikaryons. These are, quite simply, (1) by division of the terminal cell with its dikaryon, and (2) by division of the basal. The first typically occurs through elongation of the terminal cell and formation at its summit of a second crozier; by this process a crozier-upon-crozier series can be built up.[8] In material of *Pyronema* examined by the writer this first type of development is much the commoner of the two in the early stages of the ascogenous hyphae. According to the second, either the first-formed crozier or the side of the basal cell puts out a protuberance upon which a second crozier is formed; by this process, in its simplest manifestation, a cluster of binucleate cells is built up arranged as a strict unilateral cyme, each terminal cell having a clamp at its base, and the lumina of the basal cells being continuous with each other.[9] This type predominates in later development. But most commonly, any considerable part of a hyphal system is a combination of the two. In another way, also, the ascogenous hyphae in question are not conformable to a single pattern; for although cell-multiplication here is by hypothesis essentially multiplication of potential gonotoconts, not all the cells and dikaryons produced develop into asci; by sterilization a considerable portion is retained as merely structural elements: conducting and supporting cells; "vegetative" cells.

On the first, the crozier-on-crozier, scheme of development are based all comparisons of the clamp-hyphae of Basidiomycetes with crozier-bearing ascogenous hyphae, and all arguments for the homology of the two systems. The terminal basidium corresponds to the ascus which sooner or later puts an end to the growth of such a series of croziers; increasing sterilization of the basal segments, and increasing development of the basidiomycete diplophase as an assimilative and structural system, can account for such differences as appear in the basal portion. With the second, the cymose, scheme of development, basidial proliferation directly

[8] Cf. Claussen (**4**), *fig. 70*, left branch.
[9] Cf. Claussen, *fig. 75*, right branch.

through clamp-formation, such as occurs in the fungus here described, is as certainly, and much more obviously, homologous.

Not only the relations, but also the forms, of the comparable bodies in ascomycete and basidiomycete may be strikingly similar: for example, the beak as it first appears in *Sebacina prolifera* would seem to be almost as much a terminal recurvature, and as little a lateral branch, as the earliest hook in *Pyronema*.[10] Examination by the writer of stained material of *Pyronema* and *Ascocorticium* in which young croziers were present bears out this statement. The comparison can be carried through the complete series of stages: for example, fig. 4, 5 of this paper and Claussen's figure 76 (right), 6 and 52, 10 and 56 (right), 16 and 60, 30 and 65, 22 and 58, 20 and 59, 27 and 68 (left), 33 and 75 (right). Those who accept the homology between crozier and clamp have always held that such differences as appear are adventitious, a matter of proportion; here this difference in proportion is perhaps minimal. On the other hand, those who do not recognize the homology under discussion have chiefly considered in the Ascomycetes the cymose type of cell-multiplication, overlooking the fact that the cell-complex in either group is a mixture of the two types, and that among the Basidiomycetes the formation of basidium-bearing branches, or especially of basidia, from cells below the terminal one is always an example of the second type of development.

Objection has been made in two recent works to the homologizing of clamp and crozier. Gwynne-Vaughan & Barnes (**8**) recorded the observation that the clamp is lateral and the crozier terminal; as a matter of observation this is true. So far as the work in question is concerned, no application is made of this assertion, and no suggestion of a mode of origin of the clamp is offered. Buller (**3**) held that "the clamp-connexion may be regarded as a means for providing between any two adjacent cells of a diploid mycelium two septa instead of one and, therefore, two passage-ways [pores in the septa] for the streaming of protoplasm instead of one," while "the hook may be regarded as a means for

[10] Bensaude (**1**, p. 120) has noted a like similarity. The difference between *Pyronema* and *S. prolifera* would seem to be much less than that between the crozier described for *Humaria* (**7**, *fig. 8, 9, 11*) and that of *Pyronema* (**4**, *fig. 45, 52;* **9**, *fig. 46–49*). But cf. footnote 5.

constructing numerous ascus cells." Martin (**14**) has already recorded an objection to the bases for this distinction. The case for the functioning of septal pores in translocation is clear enough, but scarcely explains the appearance of a clamp-cell; like Buller's conjecture as to the reason for backward curvature of the beak (**3**, pp. 43–48), it is undisguised teliology. The answers to Buller's reasons for denial of the homology of crozier and clamp are already present in principle in Kniep, Bensaude, and Martens: briefly, he has over-

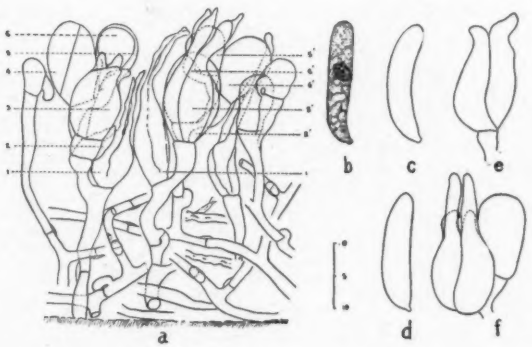


FIG. 34. *Sebacina.*

looked the crozier-upon-crozier series in the Ascomycetes and the cymose series in the Basidiomycetes, and also the biological difference between the diplophases of the two classes of fungi. The means afforded by *Sebacina prolifera* for refutation of his arguments are not more decisive, but only more obvious, than those of the authors mentioned. Buller has published four such arguments:

(1) Whereas clamp-connexions occur in series along the hyphae of a vegetative mycelium, hooks occur not in a vegetative mycelium but in the terminal branches of ascogenous hyphae;

(2) Whereas a clamp-connexion is formed in the middle of a terminal cell of a hypha, a hook is formed at the extreme end of a terminal cell of a hypha;

(3) Whereas in a clamp-connexion the cell in which a single nucleus is temporarily imprisoned is formed from a lateral branch of a main hypha, in a hook the corresponding cell is cut off from the end of the main hypha after this has become bent backwards at the apex; and

(4) Whereas clamp-connexions connect two successive cells and, as a rule, are not points of departure for new lateral branches, the end-cell of each hook, after fusion with the third cell from the end of the hypha, immediately grows forward to form a new very short branch which in turn soon becomes hooked at its apex.

Now not one of these contrasts presents any obstacle to the homologizing of the structures in question; for (1) the clamp-mycelium is not a purely "vegetative mycelium," but, like the ascogenous hyphae, the bearer of gonotoconts as well; (2) in the basidial primordia of *Sebacina prolifera* the clamp-connection is not formed "in the middle of a terminal cell," but in the same position as is the crozier of *Pyronema* and *Ascocorticium;* and where the difference does exist, it is accounted for by Martens's hypothesis; (3) the beak described in *S. prolifera* is as little a "lateral branch" and as much "the end of the main hypha . . . bent backards" as the crozier of *Pyronema;* furthermore, in a discussion of comparative morphology such as this the question of lateral or terminal origin may be precisely the subject of the enquiry, a question to be settled by comparative morphology; whether the binucleate cell from which ascus or basidium may develop is the apex of the hypha or the apex of an angle in the hypha is the point at issue; to call the clamp-beak "lateral" in such a discussion is a begging of the question[11]; and (4) clamp-connections and croziers both invariably connect successive cells; both are frequently, but not invariably, points of departure for lateral branches[12]; the clamp described in *S. prolifera* and some croziers proliferate from the beak-cell in the same fashion; other clamps and other croziers do

[11] The case is comparable to questions arising in study of the morphology of spermatophyte inflorescences.

[12] Cf. Bensaude (1), p. 85, *fig. 18;* Kniep (10), p. 383, *text-fig. 9, 10,* and the examples there cited by Kniep; also (11), p. 86, *text-fig. 2.*

not do so, proliferation being from the binucleate cell beyond the beak; still others proliferate from the stipe.

This statement at great length of an argument that must be fairly obvious has been presented only because the somewhat more elliptical discussions of the authors of the hypotheses here defended have resulted in some cases in incomplete understanding of the grounds of their argument. It is quite clear that nothing fundamental has been added to these hypotheses; that the significance of the phenomena here reported in *Sebacina prolifera* lies not in any contribution which these phenomena can make to an already essentially complete interpretation, but in exemplification of the association of the structure in question—call it clamp or crozier—in the derived group of the Basidiomycetes with its primitive function; for here, too, it serves to increase indefinitely the number of dikaryotic cells from which may be formed gonotoconts. Therefore in a largely non-reproductive hyphal system the reproductive function of the clamp-connection persists.

The hypothesis of the derivation of the clamp from the crozier is capable of one application of which little has been made: not only must the Basidiomycetes have arisen from the Ascomycetes, and from ascomycetous forms in which the ascogenous hyphae possessed croziers, but the ancestral basidiomycete group must have been one of which at least some members possessed clamps. Now all families of the lower Hymenomycetes have members whose mycelium is clamp-bearing; clamps occur in all major groups of the Homobasidiomycetes and in the smuts. Of the rusts alone no species [13] is known to have clamp mycelium. Due recognition being given the fact that an organism may be primitive in one respect and advanced in another, this deficiency even so is held by the author to support his ruling out of the Uredinales as possible ancestors for the remaining Basidiomycetes (**16**). This is the conclusion to which existing evidence may be taken to lead. In the not entirely improbable event that clamps are demonstrated in a member of the Uredinales, it may well be that the anomalous clamp-bearing rust will be the exception which tests the rival theories of the origin of the group.

[13] Disregarding the highly unconvincing figures of Voss (**17**).

SUMMARY

In *Sebacina prolifera* conjugate nuclear division at the apex of a fertile hypha is accompanied by clamp-formation. The dikaryon reconstituted in the basidial stalk by this process moves out into the enlarged clamp and there undergoes conjugate division, with the formation of a second clamp. The binucleate apical cells thus formed develop into basidia, the second basidium being borne on the clamp at the base of the first. By repetition of the process a unilaterally cymose cluster of basidia is formed. Thus among the Basidiomycetes the clamp may function in the development upon a single cell of an indefinitely large group of gonotoconts exactly as does the crozier among the Ascomycetes. This phenomenon affords additional confirmatory evidence for the hypothesis of the homology of clamp and crozier and for the derivation of Basidiomycetes from Ascomycetes. A corollary of this hypothesis and this derivation is that the ancestral Basidiomycetes must have included clamp-bearing forms.

The author desires here to record his indebtedness to the National Research Council for the fellowship during his tenure of which the present investigation was carried on; to Professor William H. Weston, Jr., and Dr. David H. Linder for suggestions and criticism during the course of the work and of the preparation of the manuscript; and especially to his wife, whose drawings illustrate the paper.

HARVARD UNIVERSITY

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DESCRIPTION OF FIGURES

All figures were drawn with the aid of a camera lucida at a magnification of 2280 × and fig. 1–33 reduced in reproduction to about 900 ×, and fig. 34 to 1000 ×. Figures are inverted—i.e., arranged with the supporting hyphae below—for more ready comparison with ascus stages. Figures are all from sections, excepting figure 34 *c-f*, drawn from preparations of crushed material.

Fig. 1–3, successive stages in the development of fertile primordium; 4, 5, formation of beak; 6, conjugate division; 7, 8, late stages of division, and basal migration of stalk nucleus; 9, reorganized nuclei; 10, completed septa; 11, 12, formation of peg for completion of clamp; 13–16, completion of clamp and basal migration of beak nucleus; 17, end of first cycle: dikaryon reconstituted in stalk; 18–21, expansion of apex of clamp, and apical movement of stalk dikaryon; 22, 23, movement of nuclei into expanded summit of clamp; 24, secondary primordium; 25, beak on secondary primordium; 26–29, successive stages in conjugate division in secondary primordium; 30, stalk dikaryon basally placed in stalk common to three basidia; 31–33, formation of tertiary primordium.

Fig. 34 *a-f: a.* Section of fruiting-layer of *Sebacina prolifera* (idealized; based on camera-lucida drawings); *b, c, d,* spores; *e, f,* basidia. In fig. *a,* basidia have arisen in the order of numbering: 1, collapsed basidium whose spores have been discharged; 2, portion of disintegrating basidium, borne on the clamp at the base of 1; 3, nearly mature basidium; 4, septate hypobasidium; 5, young probasidium, whose origin from the clamp beside 4 is clearly shown; 6, probasidium developing from the clamp of 5. On the stalk next on the right, 1′, disintegrating basidium, shrunk away from its clamp-cell on which the mature basidium 2′ is borne; 3′, probasidium formed behind 2′; 4′, probasidium borne on the clamp beside 3′, and in turn bearing 5′; 6′, clamp-cell.

NEW CONIDIAL PHYCOMYCETES DESTRUCTIVE TO TERRICOLOUS AMOEBAE

CHARLES DRECHSLER

(WITH 7 TEXT FIGURES)

In several previous papers (**1**, **2**, **3**, **4**) were described a series of conidial Phycomycetes often making their appearance on old agar plate cultures, where they subsist through the destruction of microscopic animals frequently introduced in plantings of decaying vegetable materials. Subsequent observations on laboratory cultures of the same sort have brought to light more than a dozen fungi intimately related to those dealt with before, and like them mainly parasitic or predacious on terricolous *Amoebae*. Most of the additional species are as yet only partially known. Some have been seen only as predacious mycelia devoid apparently of both conidial and sexual apparatus. Others have been observed properly only in their asexual reproductive phases, the delicate underlying mycelia at the time of observation having become largely invisible from the very evacuation of protoplasmic contents entailed in the production of the conidia. Perhaps mainly also because of such obliteration, and the consequent difficulty of tracing a connection to conidial apparatus, a few forms are familiar only through their zygosporangia and zygospores. To increase the difficulties a tract of substratum is very often occupied by a number of predacious fungi, rather than by a single predacious species; so that the hyphae and reproductive bodies of several related forms frequently occur intermingled confusingly in the same area.

Besides five fungi known in all three developmental phases—vegetative, asexual and sexual—two species are described herein, which from their consistent failure hitherto to exhibit zygosporangia and zygospores, will presumably not soon reveal such structures under the conditions of cultivation so far employed. The

seven forms do not extend materially the morphological scope of the Zoopagaceae, all being readily referable to genera previously defined. They afford, however, clarification of a few structural details. Thus the separation of zygospore wall into an outer stellate membrane and an inner spherical one, prevailing apparently throughout the genus *Endocochlus,* is shown especially clearly in the sexual apparatus of the species to be described as *E. gigas.* Again, the description of the development of catenulate conidia, as given earlier in the account of *Cochlonema verrucosum* Drechsl., is definitely confirmed in the unusually favorable material now provided by *Zoopage nematospora.* If the confirmation leaves the homologies of the conidial apparatus with the asexual reproductive structures in both the Mucorales and the Entomophthorales as problematical as ever, it makes more precise the morphological similarities to *Actinomyces* to which attention was directed earlier. Somewhat curiously, these similarities might perhaps be considered extended in the provoking even if only partial correspondence between the conspicuously simplified sexual development in *Zoopage cladosperma* and the development of the "Vierhyphensporen," which Lieske (**5**) observed in many species of *Actinomyces* and regarded as probably representing sexual structures.

ENDOCOCHLUS BRACHYSPORUS

On many old agar plate cultures that, after being found infested with various species of nematodes and protozoans, had been planted with pinches of leaf mold received from Ames, Iowa, was found on examination a week or two later, a display of arachnoid conidiiferous filaments having an unmistakable general similarity to the asexual reproductive apparatus of *Endocochlus asteroides* Drechsl. In accordance with expectations each separate system of filaments on being traced backward was found to originate from a partially or wholly evacuated cochleate thallus lying loosely within a membrane, often badly collapsed and wrinkled, that was readily recognizable as the persistent pellicle of an *Amoeba.* Living *Amoebae* bearing internally thalli in various stages of development abounded in some of the cultures (FIG. 1, *A, B*). These *Amoebae* were approximately of the same dimensions as

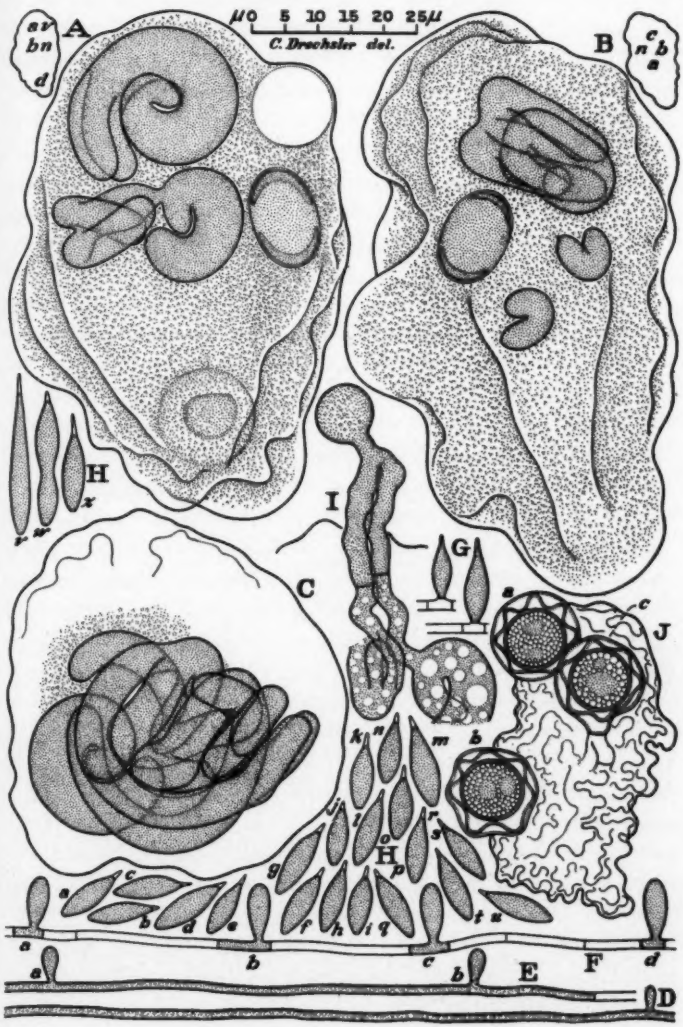

FIG. 1. *Endocochlus brachysporus.*

those attacked by *E. asteroides,* the larger specimens measuring about 60 μ in diameter when drawn up into a moderately rounded shape; they showed likewise a fairly substantial pellicle, a relatively transparent, dispersedly granular protoplasm, and a prolate ellipsoidal nucleus frequently about 15 μ long and 10 μ wide. The identity of the host animal with the form previously referred to in a broad sense as *Amoeba terricola* Greeff (and in a narrower sense as *A. terricola* I) was indicated with much certainty through the nucleus consistently revealing a slightly darker, somewhat irregularly concavo-convex body appressed closely to the peripheral membrane at each of its poles (FIG. 1, *A, n; B, n*).

Apart from the evident conspecific identity of the animals attacked, similarity to *Endocochlus asteroides* was apparent in the dimensions and involute arrangement of the vegetative thallus of the fungus itself (FIG. 1, *A, a, b; B, a-c; C*). The similarity appeared, however, to be somewhat less than complete, as in the Iowa parasite the thallus instead of always branching dichotomously sometimes gave rise to a monopodial branch (FIG. 1, *A, b*), which then developed geometrically independent of the parent axis as a subsidiary cochleate structure. That such monopodial branching may take place also in *E. asteroides* and *E. gigas* is, to be sure, not impossible; but, if so, it would seem to occur so rarely as ordinarily to escape notice.

Sexual reproduction in the Iowa parasite follows the same course as in *Endocochlus asteroides* (FIG. 1, *I*); the resulting zygosporangium and zygospore (FIG. 1, *J, a-c*) being apparently slightly larger than the homologous structures in the latter species, which, nevertheless, they closely resemble. As in the other known members of the genus, the zygosporangial wall usually collapses perceptibly when the maturing zygospore contracts—this contraction gradually bringing about the stellate contour of the outer zygospore membrane, which ultimately appears to become well separated from the smoothly spherical inner membrane immediately surrounding the protoplast.

The aerial conidiiferous hyphae growing out from the thallus of the Iowa fungus (FIG. 1, *D, E, G*) give rise to conidia through lateral budding in much the same manner as those of *Endocochlus asteroides.* A fairly conspicuous difference soon appears, how-

ever, in the consistently closer spacing of the conidia on the parent hyphae (FIG. 1, *F*). Correlated with this closer arrangement, the conidia on maturity are noticeably smaller, the lesser bulk being accounted for through a marked inferiority in length (FIG. 1, *H*, *a-u*). The elongate ovoid shape thus brought about is easily distinguished from the more slender fusiform conidial shape characteristic of *E. asteroides*. Even though on examining a large number of conidia, a few specimens (FIG. 1, *H*, *v-x*) can be found comparable to those of the species described earlier, the general run of these bodies maintain their distinctive dimensions and shape with much constancy. The parasite is therefore described under a specific name having reference to its relatively short spore.

Endocochlus brachysporus sp. nov.

Hyphae nutritae 4–8.5 μ, semel vel bis spiraliter convolutae. Conidia fusoidea vel elongato-ovoidea, 7–15 μ (raro usque 21 μ) saepius 8–12 μ longa, 3–4.2 μ lata, in apice appendicula vacua 1–3.5 μ longa praedita, ex hyphis arachnoideis 1.3–1.6 μ crassis 1–4 mm. longis ad intervalla 25–45 μ longa enata. Zygosporae hyalinae vel luteolae, echinatae, intra zygosporangium sphaeroideum 12–15 μ diam. formatae, loculo 6.5–9 μ diam. Hyphae zygosporiferae 2.5–4 μ crassae, 25–50 μ longae.

Amoebam terricolam (sensu latiore) enecans habitat in humo silvarum, Ames, Iowa.

Vegetative hyphae 4 to 8.5 μ in diameter, simple or often when well developed sparingly branched dichotomously or monopodially, and compactly convoluted in 1 to 2 turns. Conidia rather broadly spindle-shaped or elongate ovoid, measuring 7 to 15 μ (rarely up to 21 μ), mostly 8 to 12 μ (average 10.2 μ) in length by 3 to 4.2 μ (average 3.5 μ) in diameter, exclusive of an empty apical appendage 1 to 3.5 μ (average 1.6 μ) long and .5 to 1 μ wide at the base; produced erect and sessile or nearly sessile at intervals of 25 to 45 μ on aerial hyphae often 1 to 4 mm. long and 1.3 to 1.6 μ wide. Zygospore colorless or slightly yellowish; at maturity bullate, the outer membrane being disposed in 15 to 20 protuberances of which about 6 are visible in the stellate profile; containing a locule 6.5 to 9 μ in diameter, surrounded by the smooth inner membrane; produced within a spherical zygosporangium mostly 12 to 15 μ in diameter arising from a short hyphal extension from the junction of paired zygophoric hyphae that measure usually 25 to 50 μ in length and 2.5 to 4 μ in width.

Destructive to *Amoeba terricola* (in the broad sense more particularly of Penard) in leaf mold from Ames, Iowa.

ENDOCOCHLUS GIGAS

The same sample of leaf mold from which was obtained the fungus just described yielded also a congeneric form much more impressive in its generous dimensions. This larger species was found to confine its attack exclusively to an *Amoeba* measuring mostly 60 to 110 μ in diameter. In its firm substantial pellicle and its transparent, dispersedly granular protoplasm the animal showed similarities to the one habitually parasitized by *Endocochlus asteroides* and *E. brachysporus,* as well as to the *Amoeba* serving as host to *Bdellospora helicoides* Drechsl. In its nucleus, however, it was markedly different from both. Viewed in optical section, this prolate ellipsoidal structure, which measured often about 20 μ in length by 13 μ in diameter, revealed the darker material as rod-like parts arranged in an interrupted ring close to the periphery (FIG. 2, *A, n; B, n; C, n*); although on focusing on the upper and lower surfaces the darker parts appeared more nearly as if connected in a continuous reticulum. Because of the close correspondence in shape and composition with the nucleus set forth as characteristic of *A. terricola* (**6**), it would seem that Greeff's binomial is applicable here in a narrower sense.

Infection is accomplished in the same manner as has been described for *Endocochlus asteroides.* Germination of an adhering conidium here likewise first results in a somewhat swollen protuberance that clearly betrays its character as an appressorium by its easily visible coating of yellowish adhesive material (FIG. 2, *A, a*). In spite of this adhesive material, the animal sometimes must manage to disengage itself successfully, as a living detached conidium is occasionally to be found bearing an empty appressorium with an empty incipient germ tube (FIG. 2, *K*). When no mishap intervenes the germ tube penetrates well towards the center of the animal, often taking a somewhat irregular course (FIG. 2, *A*). With the disarticulation of the swollen body resulting from the migration of the conidial contents to the tip of the germ tube (FIG. 2, *B, a, b*), appropriation of the substance of the host begins. The animal endures the continuing depletion of its protoplasm with remarkable fortitude (FIG. 2, *C*), but finally succumbs when the small residue of cytoplasm together with the visibly degenerating

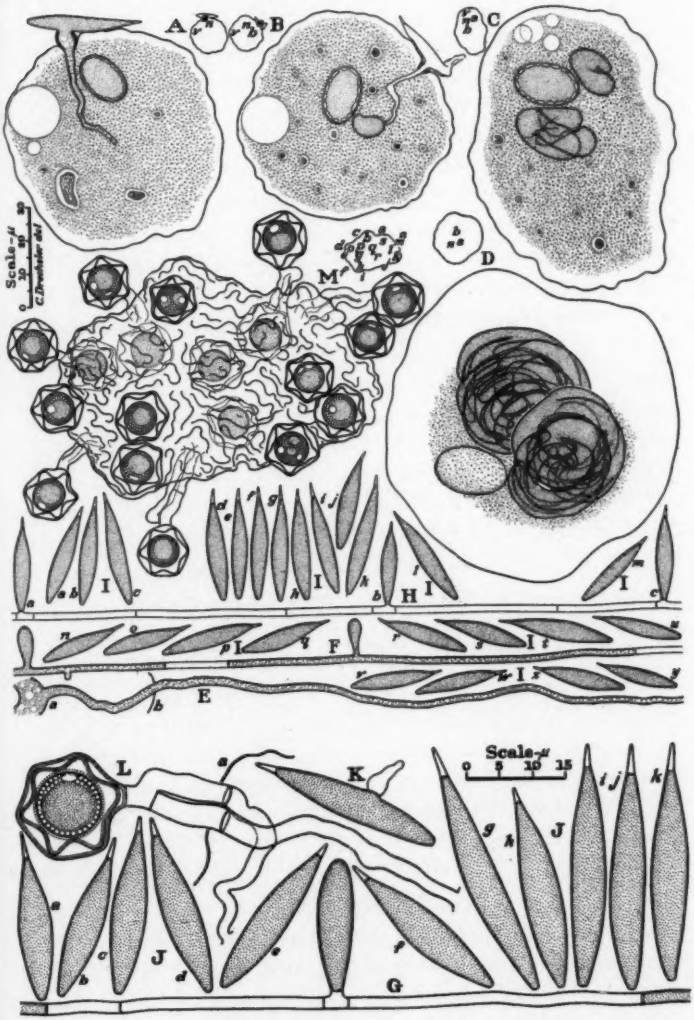

FIG. 2. *Endocochlus gigas.*

nucleus (FIG. 2, *D, n*) is no longer able to actuate the relatively little diminished pellicle.

Owing no doubt to the large supply of food material in the massive sarcode of the host animal, the thallus of the present fungus often attains a size never observed to be equalled in *Endocochlus asteroides* and *E. brachysporus*. The two impressive thalli shown in figure 2, *D, a, b,* each consisting of a stout filament bifurcating three times in succession and coiled in three turns, are yet individually of smaller bulk than a thallus developing alone in a host animal of comparable or, perhaps, even larger dimensions. Just as in the two congeneric forms, the contents of the thallus must be of extraordinary concentration; for the output of reproductive apparatus, whether sexual or asexual, is always far in excess of what might reasonably be expected from the volume of the vegetative structure from which it arises.

The hyphae associated with asexual reproduction, including the usually submerged and sterile proximal portions (FIG. 2, *E*) as well as the aerial or somewhat prostrate conidiiferous prolongations that radiate for several millimeters above the dead host animal, are noticeably stouter than the corresponding elements of *Endocochlus asteroides* and *E. brachysporus*. The conidia, half again as wide and nearly three times as long as those of *E. brachysporus,* arise at intervals approximately three times as long as the intervals in that species (FIG. 2, *F–H*). As in the two congeneric species the apex of the conidium is evacuated toward maturity and persists as an empty conical appendage (FIG. 2, *H, a-c; I, a-y; J, a-k*). Considered by itself the spindle-shaped living cell is rather similar in size and shape to the living cell in the conidium of *Acaulopage ceratospora* Drechsl.

Sexual reproduction would seem, in general, more abundant than in *Endrochlus brachysporus*. As many as 24 zygospores have been found clustered about the collapsed pellicle of what before must have been an unusually large animal; therefore the output represented in figure 2, *M, a-s,* consisting of 19 such spores cannot be considered extreme. The zygosporangia and zygospores are noticeably larger than those of the two known congeneric species; so that the separation of the stellate outer zygospore membrane from both the enveloping zygosporangial wall and the spher-

ical membrane surrounding the locule is more clearly evident (FIG. 2, *L*). Within the locule the arrangement of contents widely prevalent in oospores is recognizable: an elliptical refringent body, or sometimes two such bodies, being imbedded in the parietal layer of uniformly coarse granules that surrounds the relatively large, vacuole-like reserve globule.

A term having reference to the large dimensions of the fungus is deemed appropriate as a specific name.

Endocochlus gigas sp. nov.

Hyphae nutritae 3.5–9.5 μ diam., bis vel ter spiraliter convolutae. Conidia fusoidea, 21–36 × 4.4–6.2 μ, in apice appendicula 2.2–5 μ longa praedita, ex hyphis arachnoideis 1–5 mm. longis 1.8–2.3 μ crassis ad intervalla 80–130 μ longa enata. Zygosporae hyalinae vel luteolae, echinatae, intra zygosporangium sphaeroideum 13–17 μ diam. formatae, loculo 8–10 μ diam. Hyphae zygosporiferae 1.5–4 μ crassae, 25–60 μ longae.

Amoebam terricolam (sensu strictiore) enecans habitat in humo silvarum, Ames, Iowa.

Vegetative hyphae 3.5 to 9.5 μ in diameter, when well developed often bifurcating 3 times in succession and convoluted compactly in 2 to 3 or even 3½ turns. Conidia spindle-shaped, measuring 21 to 36 μ (average 28 μ) in length by 4.4 to 6.2 μ (average 5.1 μ) in diameter, exclusive individually of an empty pointed apical appendage 2.2 to 5 μ (average 3.6 μ) long and .8 to 1.2 μ wide at its base; produced erect and sessile or nearly sessile at intervals of 80 to 130 μ on aerial hyphae 1 to 5 mm. long and 1.8 to 2.3 μ wide, that ramify more or less to extend over the substratum in a somewhat arachnoid pattern. Zygospore colorless or slightly yellowish, its outer membrane disposed in 15 to 20 bullate protuberances of which usually 6 or 7 are visible in the stellate profile, its smooth inner membrane surrounding a subspherical locule 8 to 10.5 μ in diameter; produced within an originally subspherical zygosporangium measuring 13 to 17 μ in diameter and borne on a short hyphal extension from the junction of zygophoric hyphae 1.5 to 4 μ wide and 25 to 60 μ long,—the zygosporangial wall at maturity collapsing loosely about the bullate zygospore membrane.

Destructive to *Amoeba terricola* (in a stricter sense) in leaf mold from Ames, Iowa.

ACAULOPAGE CERCOSPORA

A fungus readily referable to the genus *Acaulopage* made its appearance several times on old agar plate cultures to which had

been added pinches of muck originating from near South Bend, Indiana. Like the other members of the genus it subsists on *Amoebae,* the animals captured by it, mostly 10 to 20 μ in diameter, belonging evidently to a single species. As no nucleus could be distinguished in the peculiarly turbid and mostly homogeneous protoplasm bounded by the very delicate, scarcely visible pellicle, the identity of the prey could not be determined. The materials composing the smaller animals are usually assimilated by means of a single haustorium, consisting of a stalk together with several wider elements branching from it (FIG. 3, *A, a; B; C; E*). Larger animals, however, often occasion the production of two (FIG. 3, *D*) and sometimes three or four haustoria, especially when capture takes place at the junction of two branches (FIG. 3, *A, b*), or where two filaments happen to lie near one another.

Closely resembling the haustorial stalks in dimensions, the sterigmata on which the conidia are borne singly arise erect from the prostrate superficial hyphae (FIG. 3, *C–I*) at rather close intervals. Though the sterigmata and the fertile hyphae together have an appearance suggestive of the homologous structure in *Acaulopage macrospora* Drechsl., the simility is not extended to the conidia, which consist here individually of a rather small elongated ellipsoidal living cell bearing distally a relatively long, narrow, empty appendage (FIG. 3, *E–I*). Conspicuous differences from the conidium of *A. ceratospora* are evident in the much smaller dimensions throughout and in the absence of a basal appendage. When viewed under a dry objective, the conidia, bristling in close linear arrangement in an open arachnoid pattern corresponding to the disposition of the prostate hyphae, present a most distinctive appearance.

Sexual reproduction has never been observed. A term having reference to the tail-like conidial appendage would seem appropriate as specific name for the fungus.

Acaulopage cercospora sp. nov.

Paulo sparsa; hyphis incoloratis, 1–1.7 μ crassis; haustoriis ex stipe et 4–6 lobulis vel ramulis divaricatis 1.2–2 μ crassis compositis. Conidia solitaria, ex sterigmatibus erectis 2–5.5 μ altis orta, hyalina, appendiculata: Cellula viventi protoplasmatis repleta, fusoidea vel elongato-ellipsoidea, 7–15 μ

longa, 2.2–3.6 μ crassa, appendicem apice ferente; appendice vacua, angustata, 6–20 μ longa, .4–.8 μ crassa, in aere saepe marcida. Zygosporae ignotae.

Habitat in humo palustri, *Amoebas* 10–20 μ latas capiens et consumens, prope South Bend, Indiana.

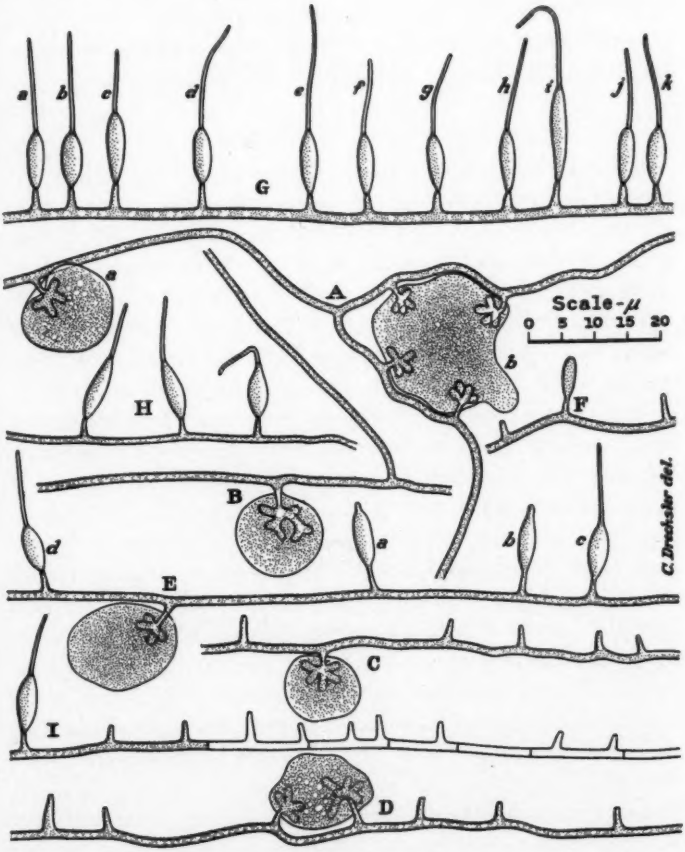

FIG. 3. *Acaulopage cercospora.*

Somewhat sparse; hyphae colorless, 1 to 1.7 μ wide, producing stalked haustoria with 4 to 6 spreading lobate or digitate elements mostly 1.2 to 2 μ wide. Conidia hyaline, solitary; borne on erect, somewhat tapering sterigmata, 2 to 5.5 μ high, that arise at intervals of 5 to 30 μ from superficial prostrate filaments; consisting

individually of a living fusoid or elongated ellipsoid cell 7 to 15 μ (average 9.1 μ) long and 2.2 to 3.6 μ (average 2.8 μ) wide, together with an empty narrow distal appendage, often withered on exposure to air and measuring 6 to 20 μ (average 12.2 μ) in length by .4 to .8 μ in width.

Occurring in muck soil near South Bend, Indiana; capturing and destroying *Amoebae* mostly 10 to 20 μ in diameter.

STYLOPAGE RHABDOSPORA

A species of *Stylopage* different from any of the four forms hitherto assigned to that genus appeared in a few old agar plate cultures on which had been planted pinches of leaf mold collected in a wooded tract in Clarendon, Virginia. In all instances it subsisted apparently altogether by the capture of *Amoebae* undoubtedly referable to a single species. The animal taken measured mostly from 30 to 40 μ in diameter when drawn into an approximately round shape. Except for a sappy homogeneous layer immediately under the delicate pellicle, the protoplasm consisted of rather densely and coarsely granular material, which was nevertheless sufficiently transparent to reveal very clearly a single prolate ellipsoidal nucleus mostly 9 to 10 μ in length and 7 to 8 μ in diameter (FIG. 4, *A, a, b; C*). In optical section this nucleus revealed close under its own membrane about a dozen subspherical masses of slightly darker material. The nuclear structure represented here thus corresponds to that which Penard (**6**) once figured as being characteristic of an *Amoeba* he considered probably identical with *Amoeba similis* Greeff. Adoption of the binomial mentioned has at least the advantage of setting the animal in question apart from any of the four forms to which I have referred as *A. terricola.*

The mycelium of the fungus is rather sparse, being composed of filaments that often traverse relatively long distances in a nearly straight line without giving off any branches. When contact with a susceptible *Amoeba* has been effected, a delicate process is thrust through the pellicle some distance into the protoplasm, there widening abruptly and branching dichotomously with a variable degree of regularity, and thus giving rise to a haustorium comparable, for example, to that of *Acaulopage macrospora* (FIG. 4, *A, a, b*). De-

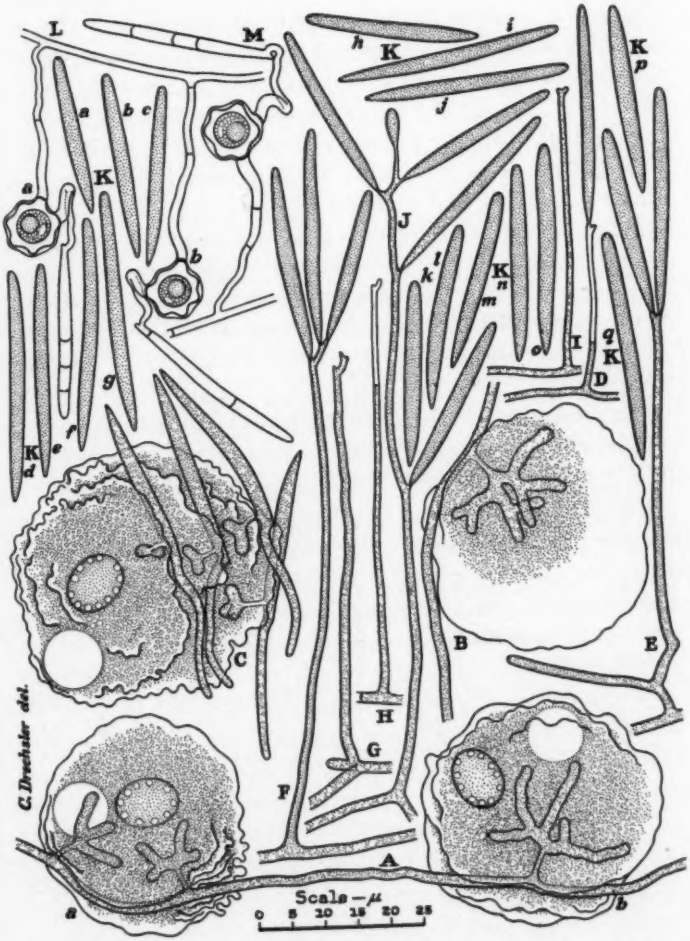

FIG. 4. *Stylopage rhabdospora.*

pletion of the protoplasmic materials of the rhizopod continues until little remains but the pellicle (FIG. 4, *B*).

Haustoria are often produced also by adhering conidia when an animal has had the ill fortune to encounter one or often several of these bodies in moving over the surface of a substratum strewn with them (FIG. 4, *C*). In performance, therefore, and, indeed, in general appearance as well, the conidia (FIG. *K, a-g*) recall those of *Acaulopage macrospora;* differing from them, however, in their smaller dimensions and in being borne on hyphae of sufficient height to deserve to be regarded as conidiophores (FIG. 4, *E–J*). After giving rise to one conidium, these conidiophores, like the homologous structures of *Stylopage lepte* and *S. hadra,* often produce others following repeated prolongation below successive spores in the manner of development made familiar in *Phytophthora infestans* (Mont.) de Bary.

The production of a haustorium directly from a conidium does not preclude simultaneous production of a vegetative germ hypha (FIG. 4, *C*). In instances where a conidium germinates by giving rise directly to a zygophore (FIG. 4, *L, M*), the protoplasmic contents are usually contributed in their entirety to the resulting sexual apparatus. Just as in similar sexual development already noted in some related forms, the progressive evacuation of the conidium is generally accompanied by the laying down of a number of successive cross-walls.

Sexual apparatus is formed in moderate quantity wherever the fungus attains any considerable growth, pairs of zygophoric branches arising either from separate hyphae having no close mycelial connection with each other, or from a hypha and a conidium, or from two conidia. Fusion of the sexual branches at their tips, development of a spherical zygosporangium at the junction, delimitation of the fusion cell by septa, and transformation of its contents into a yellowish zygospore with a relatively thick bullate wall, show unmistakable parallelism with sexual development in related species such as *Zoopage phanera* Drechsl. and *S. lepte.* Indeed, as the latter congeneric form was present in quantity in all cultures wherein the fungus under discussion was found, the structural parallelism between the intermingled sexual reproductive

bodies was evident to a troublesome degree. The dimensional differences, to be sure, were in nearly all cases, sufficient to distinguish the product of the one species from that of the other; though in choosing specimens for illustration it was thought advisable to obviate the possibility of error by selecting only unambiguous apparatus originating at least partly from conidia.

A term having reference to the rodlike shape of the conidium is deemed tolerably appropriate as specific name for the fungus.

Stylopage rhabdospora sp. nov.

Sparsa; hyphis sterilibus incoloratis, 1–1.8 μ crassis, haustoria pedicellata evolventibus; pedicello saepius .6–.8 μ crasso, 2–4 μ longo, ramulis dichotomis, divaricatis, 1.2–2 μ crassis, usque 15 μ longis; hyphis fertilibus incoloratis, 20–100 μ altis, basi .8–1.5 μ crassis, sursum saepe paulatim attenuatis, apice .6–1.2 μ crassis, usque 4 conidia post incrementa brevia repetita ferentibus. Conidia elongato-cylindracea, sursum leniter attenuata et abrupte rotundata, deorsum plerumque attenuata, itaque basi acutiuscula, 22–38 μ longa, 2.2–2.8 μ lata. Zygosporangia primo levia, sphaeroidea, 7.5–9.5 μ diam., in maturitate membrana circa zygosporam collabente; zygospora flavida, sphaeroidea, 6.5–8.5 μ diam., membrana .7–1.7 crassa, 10–20 verrucis ornata.

Habitat in materiis plantarum putrescentibus, praecipuo in humo silvarum, *Amoebam similem* capiens et consumens, Clarendon, Virginia.

Sparse; vegetative hyphae colorless, 1 to 1.8 μ wide, producing haustoria composed individually of a stalk mostly .6 to .8 μ wide and 2 to 4 μ long, together with spreading, irregularly dichotomous branching elements 1.2 to 2 μ wide and up to 15 μ long; fertile hyphae colorless, 20 to 100 μ high, .8 to 1.5 μ wide at the base, usually tapering gradually to an apical width of .6 to 1.2 μ, bearing mostly from 1 to 4 conidia, of which those following the first are formed after repeated, usually rather slight elongation. Conidium elongated cylindrical, generally tapering rather slightly toward the abruptly rounded apex, and more markedly toward the somewhat acute base, 22 to 38 μ, mostly 25 to 35 μ (average 30 μ) long, and 2.2 to 2.8 μ (average 2.5 μ) wide. Zygosporangium at first smooth, spherical, 7.5 to 9.5 μ in diameter, its wall at maturity collapsing loosely about the zygospore; zygospore yellowish, subspherical, 6.5 to 8.5 μ in diameter, with a wall, .7 to 1.7 μ thick, ornamented with 10 to 20 wartlike protuberances, of which 6 to 8 are visible in the sigillate profile.

Occurring in decaying plant materials, especially in leaf mold, capturing and consuming *Amoeba similis,* Clarendon, Virginia.

ZOOPAGE ATRACTOSPORA

The leaf mold from Ames, Iowa, that gave rise to *Endocochlus brachysporus* and *E. gigas*, yielded in nearly all of the old agar plate cultures to which it was added, flourishing growths of a fungus immediately recognizable as a species of *Zoopage*. The plate cultures used were infested very abundantly with a species of *Amoeba* measuring mostly 12 to 25 μ in diameter when drawn into a fairly rounded shape. In the normal animal a pellicle could hardly be recognized, though an individual depleted largely of its protoplasmic material generally revealed a very delicate envelope (FIG. 5, *B*). Very probably because of the characteristic turbidity of the protoplasmic body, no nucleus, nor, indeed, any normal structure except a relatively small contractile vacuole could be definitely made out (FIG. 5, *A; C; D; G, a*); the animal thus showing a general similarity to the one captured by *Acaulopage cercospora*. On this protozoan the fungus subsisted evidently to the exclusion of other sources of nourishment, capture being effected by adhesion to submerged as well as superficial hyphae, and assimilation being accomplished by means of haustoria bearing individually a half dozen divergent elements on a slender stalk (FIG. 5, *A–D; G, a*).

Nourished from an extraordinarily abundant supply of *Amoebae* the fungus gave rise to a tangled profusion of conidial chains that often extended over large areas of the plate cultures and became visible to the naked eye as a delicate efflorescence. Perhaps most of the chains consisted of approximately 10 spores, though many were found containing more than twice that number. As in *Zoopage phanera* the young chains are represented by continuous, somewhat moniliform filaments constricted at fairly regular intervals. The presence frequently of a minute swollen bud at the tip of an elongating moniliform filament (FIG. 5, *E, F*) supplies good evidence that increase of swollen components ensues through successive proliferation from the constricted apex of the component last completed. After the filament has attained its definitive length, the insertion of two crosswalls a short distance from one another in the narrowest part of each isthmus, preceded presumably by evacuation of the very minute constricted section, brings about the conversion of the swollen components into separate conidia (FIG. 5, *C, b; E, b*). Though most of the conidia

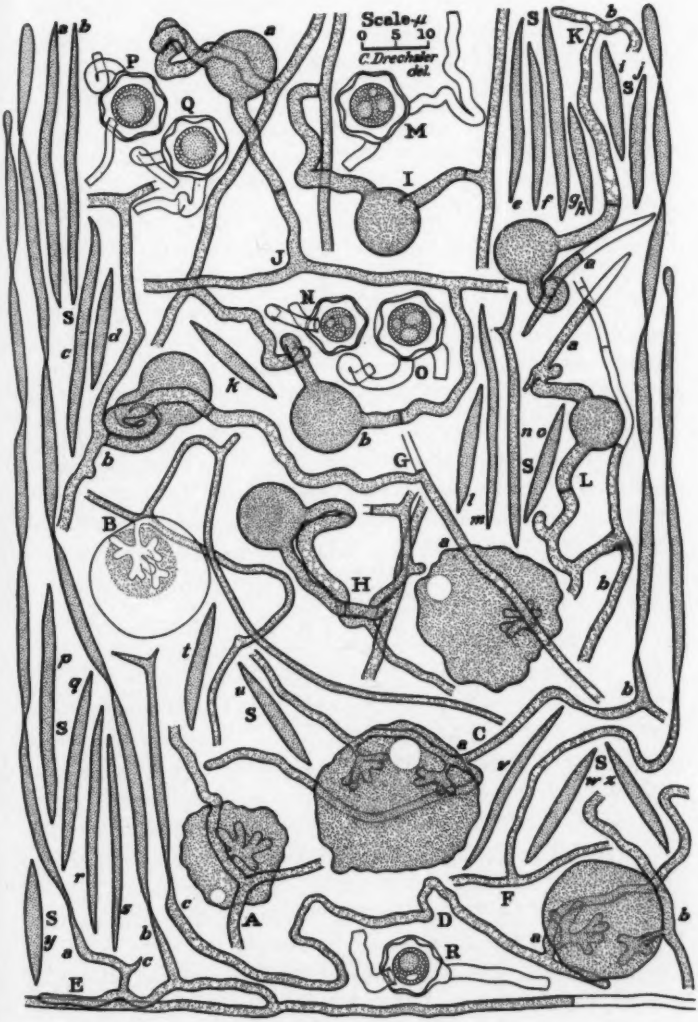

FIG. 5. *Zoopage atractospora.*

(FIG. 5, *S a-y*) are rather acute at both ends the terminal conidium of each chain (FIG. 5, *C, b; E, b*) is recognizable even after disarticulation by its broadly rounded apical extremity. Branching of a chain especially near its base occurs with some frequency, resulting in occasional bifurcate conidia (FIG. 5, *C, c; S, n*). Somewhat analogous branching of the relatively short, erect sterigmata, or of the parent hyphal branches in close proximity to them, is equally frequent (FIG. 5, *E, a-c*), but is reflected merely in the spore chains arising in small groups, rather than in the shape of the spore itself.

In spite of the general resemblance of the conidial apparatus to that of *Zoopage phanera,* specific differences are easily recognized. The conidia of the present species are conspicuously shorter, and as might be expected from the smaller diameter of the mycelial hyphae, also narrower than those of the form described earlier. In *Zoopage phanera* the variation in width of conidium is relatively small; and in any particular spore, width seems little influenced by length, so that the longer specimens are also very generally proportionately bulkier. Whereas in the fungus under consideration the longer conidia (FIG. 5, *S, b, m, n, r, s, v*) are often noticeably narrower than the shorter ones (FIG. 5, *S, d, i, j, l, o, u, w, y*), variation in one dimension being, therefore, in some measure compensated by opposite variation in the other. Moreover, the verrucose sculpturing of the conidial membrane, though visible in dry preparations, is much less prominent than in *Z. phanera,* being mostly so minute that at the magnification of the accompanying figure, it could hardly be shown without considerable exaggeration.

On the other hand, the sexual reproductive structures of the fungus closely resemble those of *Zoopage phanera:* similarities being evident, for example, in the origin of zygospores from conidia (FIG. 5, *K, a; L, a*) as well as from mycelial filaments (FIG. 5, *G, b; H; I; J, a, b; K, b; L, b*); in the size of the zygosporangium and the noticeable collapse of its wall at maturity (FIG. 5, *M–R*); and in the size, coloration and bullate sculpturing of the zygospore itself (FIG. 5, *M–R*).

A term having reference to the spindle-like shape characteristic more particularly of its shorter conidia, may perhaps serve acceptably as specific name for the fungus.

Zoopage actractospora sp. nov.

Mycelium ramosum; hyphis hyalinis, saepe irregulariter flexuosis, 1–2 μ crassis; haustoriis pedicellatis, pedicello 1.5–4 μ longo, .5–1 μ crasso, 4–8 ramulos digitatos circa 1.2–1.5 μ crassos ferente. Conidia minute et imperspicue verrucosa, fusoidea vel elongato-fusoidea, interdum bifurcata, 10–45 μ longa, 1.4–2.7 μ crassa in calenulis ex apice attenuato sterigmatum brevium et interdum ramosorum oriunda, in quaque catenula quina usque vicena quina. Zygosporangia 8–11.5 μ diam., primum levia, mox paulo collabentia. Zygosporae flavida, 6.5–10 μ diam., membrana .6–1.8 μ crassa, loculo 5–6.7 μ diam.; 15–25 verrucis ornata.

Amoebas 12–25 μ latas capiens et consumens habitat in humo silvarum, Ames, Iowa.

Mycelium branched; hyphae hyaline, often following irregular haphazard courses, 1 to 2 μ wide; haustoria pedicellate, the pedicels 1.5 to 4 μ long, .5 to 1 μ wide, and bearing 4 to 8 digitate branches 1.2 to 1.5 μ wide. Conidia minutely and very inconspicuously warted, fusiform or elongated fusiform, sometimes distally forked; measuring 10 to 45 μ, mostly 17 to 37 μ (average 25 μ) in length, and 1.4 to 2.7 μ (average 2.1 μ) in width; produced in chains of 5 to 25 on tapering, short, yet sometimes branched sterigmata. Zygosporangium 8 to 11.5 μ in diameter, at first smooth, at maturity collapsing loosely about the sculptured zygospore. Zygospore yellowish, 6.5 to 10 μ in diameter, with a locule 5 to 6.7 μ in diameter and a wall .6 to 1.8 μ thick; the wall provided with 15 to 25 warty protuberances of which 6 to 8 are usually visible in the sigillate contour.

Occurring in leaf mold, capturing and consuming *Amoebae* mostly 12 to 25 μ in diameter, Ames, Iowa.

ZOOPAGE NEMATOSPORA

A species of *Zoopage* markedly different from *Z. phanera* and *Z. atractospora* developed luxuriantly in a series of old agar plate cultures to which had been added pinches of decaying vegetable matter collected by S. P. Doolittle and F. L. Wellman in a ditch at the Subtropical Experiment Station near Homestead, Florida, early in March, 1935. In these cultures it lived from all appearances exclusively on the numerous *Amoebae* that it held fast on its mycelium and depleted of substance by means of stalked haustoria whose longish digitate absorptive elements were displayed in a characteristically graceful broom-like arrangement (FIG. 6, *A*). The *Amoebae* captured measured mostly from 40 to 50 μ in diam-

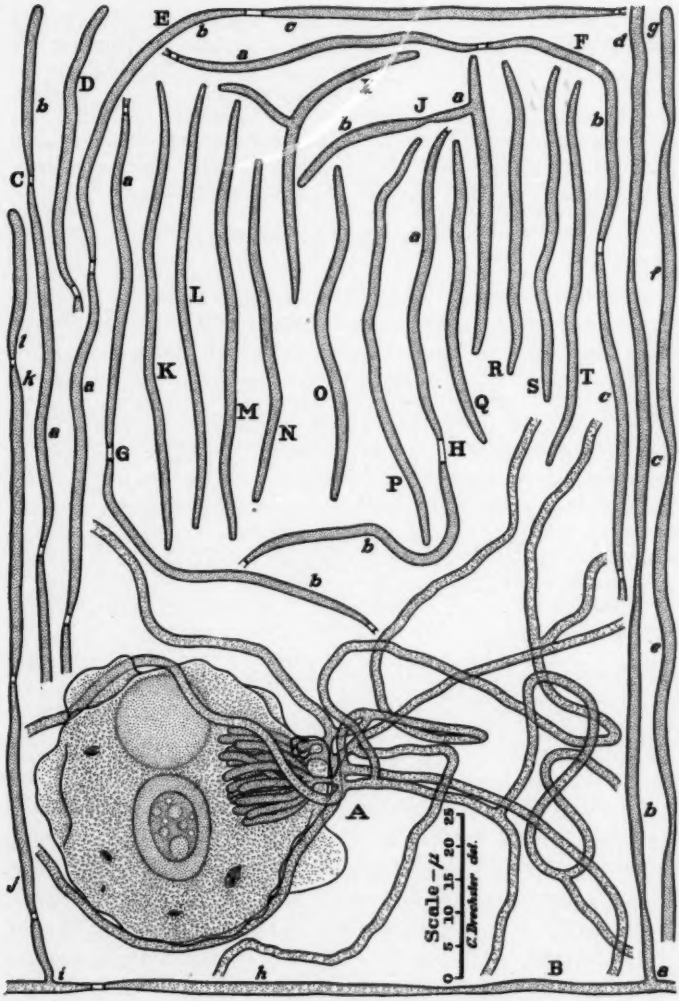

FIG. 6. *Zoopage atractospora.*

eter, and were surrounded individually by a moderately substantial pellicle. A single roughly ellipsoid nucleus, composed of an outer clearer layer and a darker ellipsoid body interspersed with a number of clearer lacunae, was visible in the flocculently granular protoplasm of the rhizopod. The dimensions of the animal, together with the shape and composition of its nucleus, would seem indicative of identity with the form discussed by Penard (**6**) under the binomial *Amoeba striata* Pen.

Aside from the distinctive design of its haustorium, the fungus shows little in its vegetative stage to set it apart from the several other known members of the genus. At times the individual hyphae pursue fairly sraightforward courses; but again, for no evident reason, they follow capricious bends. The tendency toward haphazard arrangement is expressed also in the aerial filaments devoted to asexual reproduction. These filaments reveal less differentiation from the vegetative hyphae than in other species, the narrowed parts being not only spaced at longer intervals but also constricted less, ordinarily, indeed, measuring about one-half as much in width as the intervening parts (FIG. 6, *B, a-h*). When the isthmi are evacuated of protoplasm for lengths often equivalent to twice their widths, and the protoplasts thus separated deposit a delimiting septum at each of their respective ends, the filament becomes converted into a chain of spores (FIG. 6, *B, i-l; C–H*). Ramification of the sporiferous hyphae (FIG. 6, *B, a, i*), which would seem fully as frequent as in *Zoopage atractospora,* here likewise results in occasional branched spores (FIG. 6, *I, J*). Of evident flexibility when subjected to mechanical disturbances, as, for example, in being mounted for microscopic examination, and of a relatively small diameter little given to variation except for the rather slight tapering toward the two ends, the longish conidia present a threadlike appearance that has suggested the specific name proposed for the fungus.

Zoopage nematospora sp. nov.

Mycelium ramosum; hyphis hyalinis, saepe irregulariter flexuosis, 1.1–1.9 μ crassis; haustoriis pedicellatis, pedicello 1.5–4 μ longo, .7–1 μ crasso, 5–12 ramulos digitatos, 5–13 μ longos, 1.2–1.5 μ crassos, scopis paulo similiter digestos ferente. Conidia interdum bifurcata sed saepius filiformia, utrimque paulo attenuata, flexilia, saepius 35–65 μ longa, 1.5–2.1 μ crassa, in catenulas

saepe longas simplices vel furcatas digesta, in quaque catenula usque vicena. Zygosporae ignotae.

Habitat in materiis plantarum putrescentibus, *Amoebam striatam* capiens et consumens, prope Homestead, Florida.

Mycelium branched; hyphae hyaline, often following irregular haphazard courses, 1.1 to 1.9 μ wide; haustoria pedicellate, the pedicel 1.5 to 4 μ long, .7 to 1 μ wide, and bearing in somewhat scopulate arrangement usually 5 to 12 digitate branches mostly 5 to 13 μ long and 1.2 to 1.5 μ wide. Conidia occasionally branched but more regularly filiform, rather slightly tapering at the ends, flexible, measuring 23 to 71 μ, mostly 35 to 65 μ (average 50 μ) in length, and 1.5 to 2.1 μ (average 1.7 μ) in width; produced in numbers up to 20 in usually long, simple or branched chains, wherein they are separated from one another by evacuated narrow portions of filament mostly 1 to 2 μ long and .7 to 1 μ wide. Zygospores unknown.

Occurring in decaying plant materials, capturing and consuming *Amoeba striata,* near Homestead, Florida.

ZOOPAGE CLADOSPERMA

A species of *Zoopage* somewhat smaller than any of the three congeneric forms so far described, appeared in an old agar plate culture to which had been added a few pinches of leaf mold gathered in Clarendon, Virginia. The meager development of the fungus was probably due in part to the relative scarcity of the animal on which it preyed,—an *Amoeba* measuring usually about 15 or 20 μ in diameter, with a very delicate, inconspicuous pellicle and rather turbid, slightly granular protoplasm. Capture was effected by adhesion to submerged as well as to superficial hyphae; after which the substance of the protozoan was appropriated by means of a haustorium consisting of a slender stalk and thickened dichotomous absorptive branches (FIG. 7, *A, a*).

The conidia of the fungus, though much smaller, resembled those of *Zoopage phanera* in their elongate fusiform shape and readily noticeable verrucose sculpturing (FIG. 7, *B; C, a-o*). Branching of the conidial chains, or of the erect tapering sterigmata on which they were borne, was not observed. It is possible that the absence of such branching, and also the moderate development of the simple chains (FIG. 7, *B*), may have been an expression of restricted luxuriance rather than of a definite morphological tendency.

In its sexual apparatus the species reveals a departure from the relationship prevalent not only in the genus, but throughout the family to which it belongs. A fusion of separate branches ap-

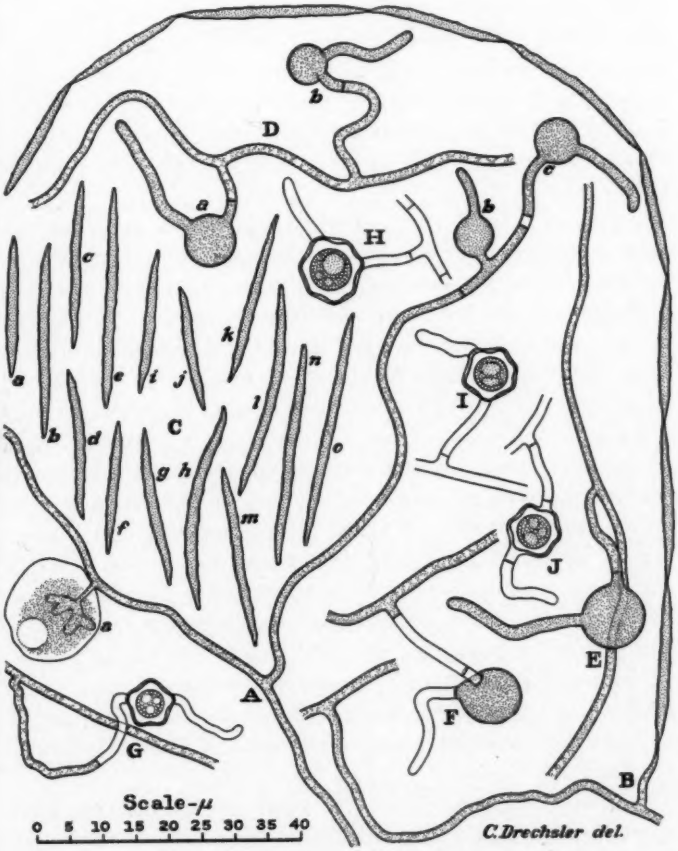

FIG. 7. *Zoopage cladosperma.*

parently never occurs. The zygosporangium makes its appearance first as a globose swelling some distance below the tip of a slightly thickened branch of limited length arising laterally from an ordinary mycelial filament. After the swelling has attained a certain

size, a septum is inserted a short distance below it, leaving the globose part still continuous distally with the apical portion of filament above it, and proximally with the portion of filament extending to the septum (FIG. 7, *A, c; D, a, b; E*). The contents of both portions of filament now pass into the globose part, which then becomes more closely delimited as a fully grown zygosporangium by the insertion of an approximately tangential septum at both of its poles (FIG. 7, *F*). Internal development ensues much as in *Zoopage phanera* and *Z. atractospora,* and yields here likewise a zygospore with bullate sculpturing and sigillate profile (FIG. 7, *G–J*).

Variations occur in the mycelial relationships of the sexual apparatus, as in instances, for example, where the proximal filamentous element consists of an intercalary segment of the axial hypha (FIG. 7, *A, b*). In any case the make-up of the very simple apparatus is such that were it found in the Mucoraceae the resultant reproductive body would almost certainly be regarded as an azygospore. In the series of predacious Phycomycetes under consideration, however, owing to the absence in declinous forms, of septa delimiting anything definitely recognizable as gametangia previous to fusion of separate hyphal tips, any distinction between an azygospore on the one hand, and, on the other, a zygospore formed presumptively through integration of portions of hypha continuous with one another from the beginning, would be much more difficult. The general analogy in development, and more particularly the passage of the protoplasmic contents of the two portions of filament into the young zygosporangium, seems to betoken a close parallelism in essential sexual processes, even though an outwardly manifest fusion entailing a breakdown of hyphal membranes is obviated.

A term having reference to the usual production of the zygospore in a special branch is deemed appropriate as specific name for the fungus.

Zoopage cladosperma sp. nov.

Mycelium ramosum, sparsum; hyphis hyalinis, 1–1.6 μ crassis; haustoriis pedicellatis, pedicello 1.5–3 μ longo, circa .7 μ crasso, aliquot ramulos dichotomos divaricatos digitatos circa 1.5 μ crassos ferente. Conidia minute sed distincte verrucosa, elongato-fusoidea, 18–36 μ longa, 1.3–1.8 μ crasso ex

apice hypharum brevium oriunda, in quaque catenula quina usque quina dena. Zygosporangia non ex copulatione hypharum separatarum sed in ramo saepius breviusculo usque 2 μ crasso sub apice ejusdem sine copulatione manifeste orta, 7–10 μ diam., primum levia, in maturitate paulo collabentia. Zygosporae flavidae, 6–8.5 μ diam., loculo 4.2–6.5 diam., membrana .6–1.5 μ crassa, 12–20 verrucis ornata.

Amoebas 15–20 μ latas capiens et consumens, habitat in humo silvarum, Clarendon, Virginia.

Myceilum branched, sparse; hyphae hyaline, 1 to 1.6 μ wide; haustoria pedicellate, the pedicel mostly 1.5 to 3 μ long and .7 μ wide bearing several bifurcating divergent digitate branches up to 1.5 μ in thickness. Conidia minutely but distinctly verrucose, elongated fusiform, 18 to 36 μ (average 26 μ) long, 1.3 to 1.8 μ (average 1.5 μ) wide, and produced in chains mostly of 5 to 15 on distally attenuated, rather short, erect branches. Zygosporangium not arising from the union of separate hyphae but developing without cellular fusion some distance below the apex of a usually rather short branch up to 2 μ wide; when fully grown 7 to 10 μ in diameter, at first smooth, later collapsing somewhat about the sculptured zygospore. Zygospore yellowish, 6 to 8.5 μ in diameter, with a locule 4.2 to 6.5 μ in diameter and a wall .6 to 1.5 μ thick; the wall provided at maturity with 12 to 20 bullate protuberances, of which 5 to 7 are usually visible in the sigillate profile.

Occurring in leaf mold, capturing and consuming a species of *Amoeba* mostly 15 to 20 μ in diameter; Clarendon, Virginia.

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EXPLANATION OF FIGURES

Fig. 1. *Endocochlus brachysporus*; drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, *Amoeba terricola* I infected with two thalli, *a* and *b*; *d*, digestive vacuole; *n*, nucleus; *v*, contractile vacuole. *B*, *A. terricola* I infected with two small thalli, *a* and *b*, as well as with a larger thallus *c*; *n*, nucleus. *C*, *A. terricola* I depleted of protoplasm by the three compacted thalli within the pellicle. *D*, *E*, *F*, Portions of conidiiferous hyphae, showing successively later stages in the formation of conidia. *G*, Conidia previous to evacuation of their respective tips. *H*, Mature conidia: *a–u* representing a random assortment; *v*, *w*, *x*, specimens unusual in length, shape and length of appendage respectively. *I*, Zygophores and developing zygosporangium. *J*, Collapsed pellicle of host animal and three mature zygospores, *a–c*.

Fig. 2. *Endocochlus gigas;* drawn with the aid of the camera lucida at a uniform magnification. *A*, *Amoeba terricola* being penetrated by a germ tube from the adhering conidium *a*; *n*, nucleus; *v*, contractile vacuole; × 500. *B*, An infected specimen of *A. terricola*, the adhering conidium *a* having become emptied in giving rise to the young thallus *b*; *n*, nucleus; *v*, contractile vacuole; × 500. *C*, A specimen of *A. terricola* containing two thalli of the parasite, *a* and *b*; *n*, nucleus; *v*, group of vacuoles about to merge into a single contractile vacuole; × 500. *D*, Dead or dying specimen of *A. terricola* with two well developed thalli, *a* and *b*; *n*, degenerating nucleus; × 500. *E*, Submerged portion of asexual reproductive filament; × 500. *F*, Aerial hypha with two conidia in early stages of development; × 500. *G*, Aerial hypha with a conidium at a somewhat later stage; × 1000. *H*, Aerial hypha with three mature conidia, *a*, *b* and *c*; × 500. *I*, Detached mature conidia, *a–y*; × 500. *J*, Detached mature conidia, *a–k*; × 1000. *K*, Conidium with an unsuccessful germ tube from which the protoplasm has been retracted; × 1000. *L*, Mature zygosporangium with attached zygophores; *a*, pellicle of host; × 1000. *M*, Collapsed pellicle of host animal surrounded with 19 mature zygospores, *a–s*; × 500.

Fig. 3. *Acaulopage cercospora;* drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, Portion of mycelium on which have been captured two *Amoebae*, *a* and *b*. *B*, Portion of mycelium with a captured *Amoeba*. *C*, *D*, Portions of hypha, each with a captured *Amoeba* and five denuded sterigmata. *E*, Portion of hypha with a captured *Amoeba*, three developing conidia, *a–c*, and a mature conidium *d*. *F*, Portion of hypha with a young conidium and two denuded sterigmata. *G*, Portion of prostrate hypha with 11 conidia, *a–k*, in place. *H*, Portion of prostrate hypha with three conidia in place. *I*, Portion of prostrate hypha consisting of an evacuated septate part with 7 denuded and evacuated sterigmata, and a living part with three sterigmata, one bearing a conidium in place.

Fig. 4. *Stylopage rhabdospora*; drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, Portion of hypha whereon have been captured two animals, *a* and *b*, referred to *Amoeba similis*. *B*, Portion of hypha with a captured animal largely depleted of protoplasm. *C*, A specimen of *A. similis* attacked by four adhering conidia. *D–J*, Conidiophores: *E*, *F*, *J*, with all spores attached; *D*, partly denuded; *G*, *H*, *I*,

wholly denuded. *K*, *a–q*, Detached conidia. *L*, Two mature zygospores, *a* and *b*, each formed from union of a zygophore arising from a mycelial filament with a zygophore arising from a conidium. *M*, Another zygospore of like origin.

Fig. 5. *Zoopage atractospora;* drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, *B*, Portions of mycelium, each with a captured *Amoeba*. *C*, Portion of mycelium with a captured *Amoeba*, *a*, and a mature chain of conidia, *b*. *D*, Portions of mycelium with a captured animal penetrated by two haustoria, *a* and *b*, and with a sterigma, *c*, bearing a bifurcate basal conidium. *E*, Portion of mycelium with one sterigma, *a*, bearing a growing aerial filament, and another, *b*, bearing a mature chain of conidia. *F*, Portion of hypha with a growing conidiiferous filament. *G*, Portion of mycelium with a captured animal, *a*, and an immature sexual apparatus, *b*. *H–J*, Immature sexual apparatus, all zygophores arising from mycelial filaments. *K*, *L*, Immature sexual apparatus, one of each pair of zygophores arising from a conidium. *M–R*, Mature sexual apparatus. *S*, *a–y*, Detached conidia.

Fig. 6. *Zoopage atractospora;* drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, Portion of submerged mycelium and a specimen of *Amoeba striata* captured thereon. *B*, Portion of aerial filament consisting of three axial components *a*, *h* and *i*, together with a young branch made up of the components, *b-g*, and a short chain of separated mature conidia, *j-l*. *C–H*, Portions of mature conidial chains. *I*, a branched conidium. *J*, A branched conidium, the part *a* perhaps still to be separated from the part *b*. *K–T*, Detached conidia.

Fig. 7. *Zoopage cladosperma;* drawn with the aid of the camera lucida at a uniform magnification; × 1000 throughout. *A*, Portion of a vegetative hypha with a captured *Amoeba*, *a*; together with a sexual branch on which two immature zygosporangia, *b* and *c*, are in process of development. *B*, Portion of hypha with a chain of mature conidia. *C*, *a-o*, Detached mature conidia. *D*, Portion of hypha with zygosporangia developing on the sexual branches, *a* and *b*. *E*, Portion of hypha with a zygosporangium developing on a sexual branch. *F*, A fully grown but immature zygosporangium. *G–J*, mature sexual apparatus with portions of mycelium showing attachments.

PHOTOGRAPHS AND DESCRIPTIONS OF CUP-FUNGI—XXIV. CHLOROCIBORIA

FRED J. SEAVER

(WITH 2 FIGURES)

The writer is proposing the above new name to replace *Chlorosplenium* as ordinarily used and for the following reasons:

Fries proposed the name *Chlorosplenium* based on *Chlorosplenium Schweinitzii* (*Peziza chlora* Schw.), a very small sessile cup-fungus of a lemon-yellow color externally and with an olive-green hymenium. The species is very common on hard wood throughout North America. Later DeNotaris, although he had never seen the type species, took up the name *Chlorosplenium* of Fries and added *Chlorosplenium aeruginosum* and *Chlorosplenium versiforme*. The former species has come to be looked upon as the typical *Chlorosplenium* although Fries did not regard it as congeneric with *Chlorosplenium Schweinitzii* when the genus was established but left it in the genus *Helotium*. Clements and Shear designate *Chlorosplenium aeruginosum* the type of the genus, giving Fries credit for the combination although, so far as we know, Fries never treated this species as a *Chlorosplenium*.

Nannfeldt recognized the fact that *Chlorosplenium Schweinitzii* and *Chlorosplenium aeruginosum* are not congeneric and suggests that the latter be kept in the genus *Ciboria*. Believing, however, that these forms are sufficiently distinct, the writer proposes that they be treated under the new name indicated below.

The following is the writer's conception of the genus *Chlorociboria* and some of the forms which should be included therein. The form on spruce cones collected by Dr. Baxter in Michigan is of unusual interest since it seems to be the first record from America.

1. **Chlorociboria** nom. nov.

Chlorosplenium DeNot. Comm. Critt. Ital. 1: 376. 1864, not Fries 1849.

Apothecia stipitate or substipitate, reaching a diameter of 1 cm. or rarely as large as 2 cm., the stem usually about half as long as

the diameter of the apothecium, resembling *Ciboria* but color green or olivaceous; asci usually 8-spored; spores irregularly ellipsoid to vermiform, simple, hyaline; paraphyses slender, clavate.

Type species, *Elvela aeruginosa* Oed.

1. **Chlorociboria aeruginosa** (Oed.) Seaver, comb. nov.

Elvela aeruginosa Oed. Fl. Dan. **9**: 7. 1770.
Peziza aeruginosa Pers. Obs. Myc. **1**: 27. 1796.
Helotium aeruginosum Fries, Summa Veg. Scand. 355. 1849.
Chlorosplenium aeruginosum DeNot. Comm. Critt. Ital. **1**: 376. 1864.
Peziza aeruginescens Nyl. Not. Fauna Fl. Fenn. **10**: 42. 1869.
Chlorosplenium aeruginescens Karst. Myc. Fenn. **1**: 103. 1871.

Apothecia gregarious, stipitate or subsessile at first cup-shaped becoming expanded and subdiscoid with the margin slightly elevated, verdigris-green and producing a similar color in the wood on which it grows reaching a diameter of 5 mm.; hymenium plane or lighter and sometimes yellowish; stem darker scarcely exceeding in length one-half the diameter of the apothecium and about 1 mm. thick; asci clavate, reaching a length of 45–50 μ and a diameter of 3–4 μ; spores 2-seriate or irregularly crowded narrow ellipsoid 2–2.5 $\times$ 5–7 μ (rarely 10–120); paraphyses very slender, about 1.5 μ in diameter, scarcely enlarged above.

On dead wood.

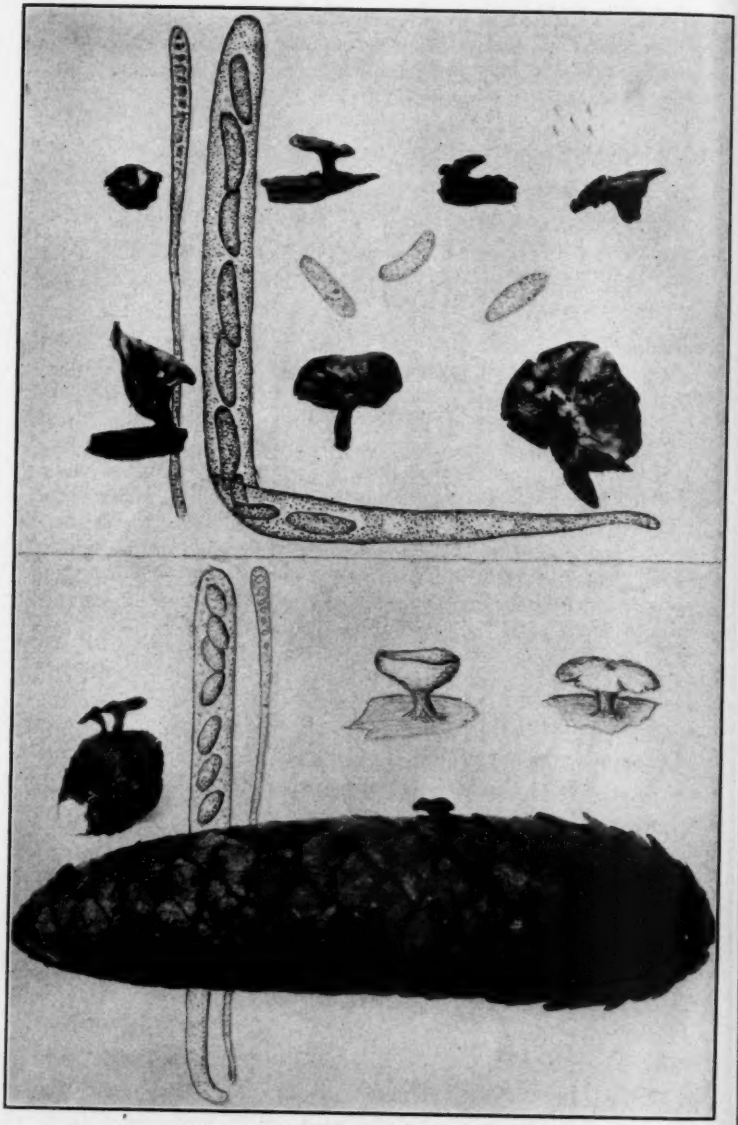
TYPE LOCALITY: Europe.

DISTRIBUTION: New York to Colorado, South to Mexico and the West Indies; also in South America, Europe, Asia, and Australia.

ILLUSTRATIONS: Boud. Ic. Myc. *pl. 485;* Fl. Dan. *pl. 534, f. 2;* Cooke, Austr. Fungi *pl. 20, f. 158;* Gill. Champ. Fr. *pl. 88, f. 1;* Grev. Scot. Crypt. Fl. *pl. 241; Bull. Lab. Nat. Hist.* **6**: *pl. 24, f. 1;* Phill. Brit. Discom. *pl. 5, f. 28;* Rab. Krypt.-Fl. 1^3: 749, *f. 1–5;* E. & P. Nat. Pfl. 1^1: *f. 155,* H–L; Massee, Brit. Fungus Fl. **4**: 156, *f. 41–42;* Sou. Engl. Fungi *pl. 347.*

EXSICCATI: N. Am. Fungi *987, 2047;* Rav. Fungi Cav. 5: *40.*

Some European authors recognize *Chlorosplenium aeruginescens* as distinct from *Chlorosplenium aeruginosum.* The writer has been unable to detect any difference of specific importance in the material which he has examined.



UPPER FIGURE. *Chlorociboria versiformis.*
LOWER FIGURE. *Chlorociboria strobilina.*

2. **Chlorociboria versiformis** (Pers.) Seaver, comb. nov.

Peziza versiformis Pers. Ic. Descr. 25. 1798.

Chlorosplenium versiforme DeNot. Comm. Critt. Ital. **1**: 376. 1864.

Helotium versiforme Berk. Outl. Brit. Fung. 372. 1860.

Coryne versiformis Rehm in Rab. Krypt.-Fl. **13**: 492. 1894.

Apothecia short-stipitate becoming expanded and subdiscoid or more often elongated on one side and often becoming subveriform; entirely light green or olivaceous, reaching a diameter of 1–3 cm.; stem short, usually not exceeding 4 or 5 mm., rather stout; asci clavate, reaching a length of 100–110 μ and a diameter of 5–7 μ; 8-spored; spores irregularly long ellipsoid straight or curved 3–4 $\times$ 9–14 μ occasionally becoming 1-septate; paraphyses strongly enlarged above where they reach a diameter of 2–3 μ, containing a greenish coloring matter.

On decaying wood.

TYPE LOCALITY: Europe.

DISTRIBUTION: New York and Massachusetts to Iowa and south to Mexico.

ILLUSTRATIONS: Boud. Ic. Myc. *pl. 486;* Bull. Lab. Nat. Hist. State Univ. Iowa **6**: *pl. 24, f. 2;* Pers. Ic. Descr. *pl. 7, f. 7;* Berk. Outl. Brit. Fung. *pl. 2, f. 6.*

EXSICCATI: N. Am. Fungi *988.*

3. **Chlorociboria strobilina** (Alb. & Schw.) Seaver, comb. nov.

Peziza tuberosa strobilina Alb. & Schw. Consp. Fung. 313. 1805.

Peziza versiformis livida Alb. & Schw. Consp. Fung. 314. 1805.

Peziza Abietis strobilina Alb. & Schw. Consp. Fung. 342. 1805.

Chlorosplenium versiforme nigrescente-olivacea Weinm. Fl. Ross. 467. 1836.

Peziza ciborioides strobilaria Nyl. Not. Fauna Fl. Fenn. **10**: 36. 1869.

Cenangium strobilinum Sacc. Fung. Ital. *pl. 1306.* 1883.

Chlorosplenium lividum Karst. Acta Soc. Fauna Fl. Fenn. II. **6**: 124. 1885.

Peziza bulgaroides Rehm in Rab. Fungi Eu. *1311;* Hedwigia **9**: 136. 1870.

Rutstroemia bulgaroides Karst. Myc. Fenn. **1**: 105. 1871.

Ombrophila strobilina Rehm in Rab. Krypt.-Fl. 1^3: 482. 1896.

Ciboria strobilina Bresadolae Boud. Ic. Myc. **4**: 18. 1907.

Apothecia stipitate or subsessile, at first concave, becoming expanded and subdiscoid or shallow cup-shaped, occasionally repand reaching a diameter of 1 cm. or rarely larger, brownish-black or with a slightly olive tint; hymenium similar in color to the outside of the apothecium; stem short scarcely exceeding one-half the diameter of the apothecium; slightly lacunose; asci clavate, reaching a length of 85 μ to 100 and a diameter of 5–7 μ; spores irregularly ellipsoid 3–4 $\times$ 7 μ.

On spruce cones.

TYPE LOCALITY: Europe.

DISTRIBUTION: Michigan; also in Europe.

ILLUSTRATIONS: Sacc. Fungi Ital. *pl. 1306;* Boud. Ic. Myc. *pl. 480.*

EXPLANATION OF FIGURES

Upper figure (1). *Chlorociboria versiformis.* Photographs of apothecia in various stages of development, about natural size; also drawings of ascus with spores and paraphysis. Photographs furnished by the Dominion National Museum, Canada.

Lower figure (2). *Chlorociboria strobilina.* Photograph of spruce cone with apothecia, about natural size; also one scale removed with apothecia. Upper right-hand corner, drawings of two apothecia, enlarged about two diameters; also drawing of ascus with spores and paraphysis. Photographed from material collected in Michigan by Dow V. Baxter.

NOTES AND BRIEF ARTICLES

The Mushroom Handbook

So many of the old mushroom books are out of print that the appearance of any new work on this subject is appreciated by mycophagists and mycologists. "The Mushroom Handbook" by Louis C. C. Krieger has recently appeared. This work was prepared at the State Museum in Albany, Dr. Krieger having previously worked with Dr. W. G. Farlow of Harvard University and Dr. Howard A. Kelly of Baltimore. The volume consists of 538 pages and is fully illustrated with halftone photographs and drawings and 32 colored plates beautifully done by Dr. Krieger. The first part of the book is devoted to a general discussion of the characteristics and habits of the fungi with directions for the growing of mushrooms. The latter part of the book consists of technical descriptions and popular notes on the various edible and poisonous species. Special attention is properly given to a consideration of the characteristics of the more poisonous species. There is, also, full discussion of common species which are safe for the beginner to use. The book is published by the Macmillan Company, New York City.—Fred J. Seaver.

Bessey's Text-Book of Mycology [1]

Those of us who had the pleasure of using Professor Charles E. Bessey's "The Essentials of Botany" in college and of knowing him personally will be especially interested in the new "Text-Book of Mycology" by his son Ernst A. Bessey.

As indicated by the author, this text is intended as an introduction to the subject of mycology, where more technical works such as Gaümann and Dodge, Comparative Morphology of Fungi are impractical. The author also emphasizes the fact that this is a text-book of morphology and not of the physiology of the fungi. Since a work of this kind will do little more than "whet the ap-

[1] Published by P. Blakiston's Son & Co., Inc., 1012 Walnut Street, Philadelphia, Pennsylvania.

petites" of budding mycologists, rather complete bibliographies by the most outstanding authors on the various groups are included at the end of each chapter.

The writer is not actively engaged in teaching of mycology but has heard very favorable reports from those who have used the text-book in their class work. This volume has been out nearly a year and it had been hoped that a more extended review might be presented by some active teacher of mycology. In the absence of this, the present announcement will suffice. The text-book is very fittingly dedicated to the memories of two great teachers, his illustrious father, Charles E. Bessey, and Georg Klebs.—F. J. SEAVER.

AN ANCIENT ROMAN TOADSTOOL CARVED IN STONE

In his article "An ancient Roman toadstool carved in stone" in MYCOLOGIA (**21**: 143–144. 1929). John W. Harshberger writes about a visit to the ruins at Timgad (Algeria), a town founded by the legate, P. Munatius Gallus, by order of the Roman emperor Trajan about 100 A.D. In the chief market place Mr. Harshberger found two large blocks of stone, one of which was "characterized by a design of *Acanthus* leaves surrounding a centrally placed stone toadstool, carved so that the gills and related stipe with basal volva are clearly shown. The stone figure has been identified as a toadstool, although with its volva, it probably represents some poisonous, pileate, lamellate, fleshy toadstool known to the ancient artist, who designed the architectural ornamentation of the Timgad market place. Do we not have in this stone carving the earliest known representation of a fleshy, gill-bearing fungus, dating back to the second century A.D.?" (Harshberger, l.c.)

When I saw the excellent photograph in MYCOLOGIA I identified the stone figure as *Volvaria speciosa* (= *V. gloiocephala*).

For a long time in Europe this fungus had been considered very poisonous, although Persoon stated that it was edible. Herrfurth in Germany, and Bresadola in Austria, ate it during the Great War, and Dearness (*Volvaria speciosa*, MYCOLOGIA **23**: 152–153. 1931) in America in 1930. The examinations of Mr. Gauthier, Menier, and Monnier have proved the fungus to be

edible. According to R. Maire's report the fungus is offered for sale in large quantities at the markets in Algeria. By the carving in stone the ancient Roman artist wanted to show a well-known merchandise, and not a poisonous fungus. I am sure the ancient Romans did not consider a pileate, lamellate, fleshy toadstool with volva to be poisonous, because their favorite mushroom, the *Amanita caesarea,* is a pileate, lamellate, fleshy fungus with volva. —HEINRICH LOHWAG, *President, Austrian Mycological Society.*

THE SYNONYMY OF BOTRYTIS RILEYI FARLOW

Botrytis Rileyi, the fungus producing the cholera disease of insects was described by Farlow in 1883 from material on larvae of *Plusia Brassicae* (*Autographa Brassicae*).[1] The spores were described as borne in whorls and catenulate and the fungus therefore can not be referred properly to the genus *Botrytis.*

In 1903, Maublanc[2] established the genus *Nomuraea* which he named in honor to Nomura who sent him specimens of *Pionea forficalis* affected by the fungus, which he called *Nomuraea prasina.* The generic description shows this fungus to be a *Spicaria,* a fact recognized by Sawada in his Descriptive Catalogue of the Formosan Fungi (1919, p. 606), the new combination being *Spicaria prasina* (Maubl.) Saw.

Petch, in one of his papers on entomogenous fungi[3] discusses *Botrytis Rileyi* and its possible identity with *Spicaria prasina* and states that the fungus on specimens of *Anticarsia gemmatilis* sent him from Florida is *Spicaria prasina.* However, mycologists in the United States have determined this fungus as *Botrytis Rileyi.*

Clements and Shear in their Genera of Fungi (1931, p. 203) separate *Nomuraea* and *Spicaria* solely on the character of their habitat, *Nomuraea* being described as entomogenous and *Spicaria* as phytogenous. This distinction does not appear to have been generally recognized, Petch and other mycologists having assigned a number of entomogenous forms to the genus *Spicaria.* In view of the close morphological affinities of *Botrytis Rileyi* with the

[1] Report of the U. S. Comm. Agr., p. 121, 1883.

[2] Maublanc, A. Sur quelques espèces nouvelles de champignons inférieurs. Bull. Soc. Myc. Fr. **19**: 295–296. 1903.

[3] Petch, T. Entomogenous Fungi. Trans. Brit. Myc. Soc. **11**: 264. 1926.

genus *Spicaria* and the priority of the specific name, this fungus should be designated as **Spicaria Rileyi** (Farl.) Charles comb. nov.—VERA K. CHARLES.

ATRACTOBASIDIUM

Under the name *Atractobasidium corticioides* Martin appeared the first recognizable description[1] of a heterobasidiomycetous fungus strikingly characterized by fusiform basidia divided by three obliquely transverse, intersecting septa. Almost immediately, as a result of what the late C. G. Lloyd was wont to call the Sacred Principle of Priority, it was found necessary to rename this fungus *A. Grandinia* (Rick) Martin.[2] It now appears that a third name must in turn replace the second.

From examination of authentic material in the Farlow Herbarium of *A. corticioides* Martin, *Platygloea Grandinia* Rick, *Patouillardina cinerea* Bres., *Protograndinia cinerea* Rick (Egatea **18**: 213), and a presumably unpublished species assigned by Rick to this genus, it is clear that all are examples of the same organism and must be known by the oldest name, *P. cinerea* Bres. The specimen of *Patouillardina cinerea,* collected by Rick in Brazil and communicated by Bresadola to Patouillard, is presumably a portion of the material discussed by Rick[3] and by Bresadola[4] and figured by the latter.[5] It is true that these discussions of *Patouillardina* completely fail to include any of the essential characters; and that the published figure, a duplicate of a sketch on the packet containing *Patouillardina* in Patouillard's herbarium, is quite insuperably delusive. It is true that from these accounts and illustrations even Rick was unable to recognize the fungus in his own later collections. Nevertheless, since no code of nomenclature permits the consigning of a name to oblivion on the mere grounds that it is founded exclusively on error, *Patouillardina cinerea* Bres. must stand until it is legally superseded by a name even longer buried and forgotten.—D. P. ROGERS.

[1] Torrey Bot. Bull. **62**: 339–343. *fig. 1, 2.* 1935.
[2] Mycologia **28**: 198. 1936 (Apr.).
[3] Brotéria **5**: 7. 1906.
[4] Ann. Myc. **18**: 52. 1920.
[5] E. & P. Naturl. Pflanzenfam. 2 Aufl. 6 Bd., *fig. 87C.*